University of Alberta

The Ecology of Polar Bears in Relation to Sea Ice Dynamics

by

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Abstract

Recent research indicates climate change will be amplified in Polar Regions, which will cause decreases to sea ice thickness and extent throughout the Arctic. Polar bears (*Ursus maritimus*) will be directly affected by changes to Arctic sea ice conditions because they rely on the ice substrate for numerous aspects of their life history. Perhaps of most importance, polar bears use the sea ice platform to access their main prey, pagophilic seals. Determining specific effects of climate-induced environmental change on polar bears will require monitoring at numerous spatiotemporal scales and across various levels of biological organization. In this dissertation I used and refined a variety of ecological monitoring tools that evaluated the effects of seasonal and longer-term unidirectional sea ice changes to various aspects of polar bear ecology. At a molecular level, I used urea to creatinine ratios in polar bear blood to show that an increased number of polar bears were in a physiological fasting state during spring captures in 2005-2006 compared to the mid-1980s. These changes corresponded to broad-scale changes in Arctic sea ice composition, which may have altered prey availability. I also used measurements of naturally occurring stable isotopes ($\delta^{13}C$, $\delta^{15}N$) in polar bear tissues to examine their diet, which included both lipid-rich blubber and the proteinaceous tissues of their marine mammal prey. Because the proportion of proteins and lipids consumed likely depended on prey type and size, it was necessary to consider metabolic routing of these macromolecules separately when using isotope mixing models to determine

and monitor polar bear diet. I also monitored polar bear movement and migration behaviour at the population level. Specific landscape sea ice metrics corresponded to seasonal population migration patterns and fidelity to particular geographic regions. Trends in the timing of these seasonal population migration patterns were likely associated with climate-induced changes to sea ice dynamics. Finally, I examined migration behaviour in relation to local sea ice dynamics in individual polar bears and demonstrated a mechanistic understanding of the relationship between sea ice and polar bear migration patterns.

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Chapter 1

General Introduction

1.1 Polar Bears, Sea Ice, and Climate Change

Polar bears (*Ursus maritimus*) evolved from grizzly bears (*U. arctos*) approximately 150,000 years ago (Lindqvist et al. 2010) when they began to exploit a niche that allowed them to utilize sea ice as a platform to access marine resources (Kurtén 1964). Consequently, the global distribution of polar bears is now concurrent with Arctic ice-covered seas (DeMaster and Stirling 1981, Amstrup et al. 1986, Durner et al. 2009). The most important habitat for polar bears is annual ice over the continental shelf and around Arctic archipelagos (Stirling et al. 1975, Stirling et al. 1993, Derocher et al. 2004). These shallow regions are the preferred habitat of pagophilic seals, the primary prey of polar bears (Stirling and Archibald 1977, Smith 1980), and are known to be the most productive marine habitats in the Arctic (Pomeroy 1997, Carmack and Macdonald 2002, Bluhm and Gradinger 2008). The sea ice represents a critical link between polar bears as an apex predator and the primary productivity supporting biologically rich Arctic marine environments (Stirling and Derocher 1993, Derocher et al. 2004). In addition to providing a necessary hunting platform (Stirling and Archibald 1977, Stirling and Derocher 1993), sea ice is also intricately linked with other aspects of the life history of polar bears such as mating (Ramsay and Stirling 1988), maternity denning in some areas (Lentfer

1975, Amstrup and Gardner 1994), and migration (DeMaster and Stirling 1981, Mauritzen et al. 2003, Durner et al. 2009).

Today, polar bears are one of the few wide-ranging large carnivores that still exist throughout most of their original range (Derocher et al. 2004). In contrast, anthropogenic habitat alteration has restricted closely related grizzly bears to less than half of their historic North American range (McLellan 1990). However, polar bears are now facing significant habitat loss as current and projected increases to mean atmospheric temperature are predicted to cause changes to the composition of sea ice and declines in its extent throughout the Arctic (Graversen et al. 2008, Boe et al. 2009, Perovich and Richter-Menge 2009). Many climate change models predict that warming induced by increases to atmospheric greenhouse gases will be amplified in Arctic regions (Hall 2004, Winton 2006). The perennial sea ice cover throughout the Arctic is declining (Comiso 2002, Nghiem et al. 2008, Comiso et al. 2008) and recent studies indicate decreases to ice thickness (Rothrock et al. 1999, Wadhams and Davis 2000, Yu et al. 2004, Maslanik et al. 2007). Declines in ice extent and thickness will have profound but difficult to predict consequences on Arctic marine ecosystems. Polar bears will most likely be directly affected by a substantial loss of important sea ice habitat and indirectly affected by bottom-up changes to ecosystem processes and trophic interactions (Stirling and Derocher 1993, Derocher et al. 2004, Laidre et al. 2008).

Reductions to the duration of coverage of annual sea ice are occurring most rapidly and extensively over continental shelf regions, where biological productivity is greatest and many pagophilic marine mammals rely upon ice-associated food sources, such as amphipods and Arctic cod (*Boreogadus saida*) (Tynan and DeMaster 1997, Bluhm and Gradinger 2008, Laidre et al. 2008). Decreases to the amount of habitat available to pagophilic marine mammals may negatively affect their reproductive success or alter their diversity and distribution (Tynan and DeMaster 1997, Ferguson et al. 2005, Laidre et al. 2008, Moore and Huntington 2008). Ringed seals (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) are common pagophilic Arctic marine mammals and the primary prey of polar bears (Stirling and McEwan 1975, Stirling and Archibald 1977, Smith 1980). Reductions in the abundance or availability of these seals will result in changes to the diet composition and feeding strategies of polar bears (Derocher et al. 2004, Thiemann et al. 2008). Changes to sea ice composition correlated with higher atmospheric temperatures have already been linked to decreases in polar bear foraging efficiencies in the Beaufort Sea (Amstrup et al. 2006, Stirling et al. 2008). Decreased accesses to prey, and the resulting nutritional stress to polar bears, are hypothesized to affect body size, survival, and breeding (Hunter et al. 2010, Regehr et al. 2010, Rode et al. 2010).

The species of seals that polar bears primarily prey upon could be affected differently by decreases in ice extent. Bearded seals may be able to adapt better to a warmer environment because they are known to occasionally haul out on land and tend to prefer areas with less consolidated ice (Stirling and Derocher 1993, Derocher et al. 2004). Ringed seals, on the other hand, breed in consolidated land-fast ice and rarely haul out on shore (Kingsley and Stirling 1991, Furgal et al. 1996, Frost et al. 2004). Early spring break-up and reduced breeding habitat can negatively affect ringed seal pup development (Smith and Harwood 2001). Furthermore, unusual rain events induced by warm temperatures can cause ringed seal birth lairs to collapse, and thus negatively affect pup survival (Stirling and Smith 2004). The diets of polar bears will likely shift to reflect any changes to the abundances of their prey species and may also begin to include species that move their ranges northward in response to climate-induced environmental changes (Tynan and DeMaster 1997, Thiemann et al. 2008).

Climate-induced changes to sea ice are also likely to affect the movement patterns and spatial distribution of polar bears (Vibe 1967, Schliebe et al. 2008, Durner et al. 2009). In southerly polar bear subpopulations, such as those in Hudson Bay, bears migrate to land when the sea ice completely melts during the summer. Throughout this time, bears fast and rely on endogenous fat reserves (Lunn and Stirling 1985, Ramsay and Stirling 1988, Stirling and Derocher 1993) because they are unable to access seals without the sea ice platform (Stirling and Derocher 1993, Ferguson et al. 2000, Derocher et al. 2004). Earlier sea ice break-up associated with climate warming forces bears to move to on-land refugia relatively earlier than normal (Stirling et al. 1999). Earlier sea ice break-up in Hudson Bay has been correlated with decreases to polar bear body condition, reproduction, and population numbers because of reductions to the on-ice feeding period and extensions to the on-land fasting period (Stirling et al. 1999, Regehr et al. 2007). Extended fasting periods have also been significantly correlated with increases to problem bear occurrences in and around the community of Churchill

(Towns et al. 2010). In addition to altering when polar bears move on and off land, climate-induced changes to sea ice break-up and freeze-up patterns may also affect fidelity of polar bears to specific coastal regions during the summer and consequently alter subpopulation boundaries (Derocher et al. 2004).

1.2 Monitoring Polar Bears in a Changing Climate

Ecological monitoring is the repeated measurement of physical, chemical, or biological parameters with the intention of answering specific questions about environmental change (Lovett et al. 2007). With current and projected climate-induced environmental change to polar bear habitat, monitoring programs are imperative for understanding specific conservation requirements. Numerous threats to polar bears have been predicted as a result of continued warming (i.e., Stirling and Derocher 1993, Derocher et al. 2004, Stirling and Smith 2004, Stirling and Parkinson 2006, Crompton et al. 2008, Laidre et al. 2008, O'Neill et al. 2008, Schliebe et al. 2008, Wiig et al. 2008, Durner et al. 2009, Molnár et al. 2010). Monitoring trends in wildlife population abundance and geographic distribution is a significant component of most management and conservation strategies (Wilson and Delahay 2001, Nichols and Williams 2006, Marsh and Trenham 2008). A key element of monitoring and managing polar bears throughout the circumpolar Arctic involves frequent abundance estimates for various subpopulations (Aars et al. 2006). Trends in population numbers are critical to managing harvest quotas and provide essential indications of overall population viability (Pollock et al. 2002, Hauser et al. 2006). However, it may be difficult to make appropriate management and conservation decisions when underlying ecological factors responsible for observed trends are poorly understood. Therefore, in addition to monitoring population trends, effective monitoring strategies that target specific hypothesis-driven questions regarding how animals may respond to potential or actual changes in their environment are desirable (Yoccoz et al. 2001, Krebs and Berteaux 2006, Lindenmayer and Likens 2010). Experimental manipulations aimed at hypothesis testing are rarely possible when examining how large-scale ecological phenomena, such as unidirectional climate change or cyclical phenological events, affect wildlife populations. However, understanding how populations and individuals respond to changes in their environment is essential for effective and responsible management decisions or conservation recommendations, regardless of whether they are related to local harvest quotas or global policies regarding climate change initiatives. Therefore, an approach that seeks to test theories regarding environmental change and ecological relationships through multiple layers of observation is a necessary aspect of monitoring (Pickett et al. 2007, Sagarin and Pauchard 2010).

1.3 Study Subpopulations and Monitoring Opportunities

In many cases, long-term data is necessary for monitoring programs designed to determine the ecological effects of climate change, which often acts on large spatiotemporal scales (Krebs and Berteaux 2006). However, understanding the ways in which species react to seasonal variation may also provide valuable information that can be used to predict responses to climate-induced environmental changes over longer timeframes. The focus of my dissertation was to evaluate multiple novel techniques for monitoring the ecology of polar bears in relation to climate change and sea ice dynamics. I used a combination of observational monitoring methods to examine how polar bears respond to both long-term unidirectional and short-term cyclical environmental changes. I examined several specific questions regarding the ecology of polar bears in relation to sea ice dynamics using a variety of ecological tools ranging from physiological biomarkers (Chapter 2) and intrinsic chemical tracers (Chapter 3) to satellite movement data (Chapters 4 and 5). The results of my dissertation provide additional tools and document initial trends arising from monitoring changes to the ecology of polar bears from the molecular to the population level.

There are 19 relatively discrete polar bear populations distributed across the circumpolar Arctic (Figure 1.1). Research for my dissertation took place in two distinct study areas: 1) the Beaufort Sea, Northwest Territories and 2) Hudson Bay, Manitoba. In the Beaufort Sea I examined two different subpopulations (Northern Beaufort and Southern Beaufort). In Hudson Bay my research focused on one subpopulation (Western Hudson Bay).

The Beaufort Sea extends northeastward from Point Barrow, Alaska to Prince Patrick Island and Banks Island, Northwest Territories (IUCN/SSC Polar Bear Specialist Group 2006). Satellite telemetry data (Taylor and Lee 1995, Bethke et al. 1996, Amstrup et al. 2004) and microsatellite genetic analysis (Paetkau et al. 1995) suggest that there are distinct northern and southern subpopulations of polar bears occurring in the Beaufort Sea. The Beaufort Sea subpopulations were over-harvested in the mid-1960s, but have recovered since the establishment of harvest quotas in 1968 (Stirling 2002). However, polar bears in this area are facing a new set of conservation problems because the seasonal extent of sea ice in the Beaufort Sea is decreasing and shifting northward as Arctic temperatures increase (Comiso 2002). Research conducted by Environment Canada in the Beaufort Sea, which involves mark and recapture techniques for population abundance monitoring, allowed for periodic collection of polar bear blood and tissue samples from a large sample size of bears. These samples may be used to examine physiological biomarkers and intrinsic chemical tracers, such as stable isotopes, to monitor various aspects of the feeding ecology of polar bears. Shifts in diet that may occur in response to climate-induced environmental changes in the Beaufort Sea include increased scavenging from the remains of subsistence-harvested bowhead whales (*Balaena mysticetus*) (Bentzen et al. 2007, Schliebe et al. 2008) or predation upon subarctic marine mammal species that might be expanding their range northward (Iverson et al. 2006, Thiemann et al. 2008). Additionally, decreased access to seals and poorer hunting success are anticipated (Derocher et al. 2004, Amstrup et al. 2006, Stirling et al. 2008). Quantitatively examining polar bear diet and developing methods to monitor diet trends will contribute to an understanding of how environmental changes may alter the structure of Arctic marine food webs in this region.

Furthermore, assessing foraging success in relation to changes in ice conditions will provide an indication of how climate-induced environmental changes are affecting the feeding ecology and physiology of polar bears in the Beaufort Sea.

Hudson Bay is a shallow inland sea located in east-central Canada that is characterized by annual freeze-thaw cycles that coincide with seasonal temperature variability (Gagnon and Gough 2005). Polar bears in the Western Hudson Bay subpopulation show high degrees of seasonal fidelity to specific coastal regions during the summer ice-free period (Derocher and Stirling 1990, Lunn et al. 2004, Stirling et al. 2004). The high degree of seasonal fluctuation in sea ice extent throughout Hudson Bay makes it amenable to examining the effects of short-term intra-annual sea ice dynamics on polar bears. Additionally, recent changes to the freeze-thaw patterns of sea ice in Hudson Bay (Gagnon and Gough 2005, Stirling and Parkinson 2006) also make the Western Hudson Bay subpopulation suitable for examining effects of climate-induced environmental changes on the movement patterns and spatial distribution of polar bears. Long-term research conducted by Environment Canada on Western Hudson Bay polar bears allowed for comparisons of archived and recently acquired movement data from satellite-linked collars. Thus, in western Hudson Bay, it was possible to examine polar bear movement patterns and fidelity to specific geographic areas in response to both seasonal phenological events and longer-term shifts related to inter-annual sea ice dynamics.

1.4 Dissertation Outline

In Chapter 2, I used data collected from the Beaufort Sea polar bear subpopulations to examine the use of the ratio of serum urea to serum creatinine as a physiological biomarker of fasting to monitor temporal patterns in the feeding ecology of polar bears. The measurement of serum urea to creatinine ratios in the blood of polar bears can be used to determine whether they are in a physiological feeding or fasting state (Derocher et al. 1990, Ramsay et al. 1991). Male polar bears may enter this state if they are not consuming food during the breeding season and all polar bears can enter a physiological fasting state during times of food shortage (Nelson 1987, Derocher et al. 1990). I used serum urea and creatinine values from blood collected in the mid-1980s and 2005-2006 to examine temporal trends in the proportion of polar bears fasting during the spring in the Beaufort Sea. I tested the hypothesis that broad-scale changes in ice conditions throughout the Arctic Ocean (Comiso 2006, Stroeve et al. 2006, Serreze et al. 2007) negatively affect prey availability for polar bears during the spring and cause bears in the Beaufort Sea to become nutritionally stressed. I also tested the hypothesis that differences in fasting frequency may occur depending on geographic location within the Beaufort Sea (Southern versus Northern Beaufort Subpopulations) or among various demographic classes of polar bears.

In Chapter 3 I further examined aspects of the feeding ecology of polar bears in the Beaufort Sea using measurements of naturally occurring stable isotopes to estimate polar bear diet composition. Intrinsic tracers, such as stable isotopes in animal tissues, are useful for monitoring diets of wide-ranging species that would otherwise be logistically difficult to evaluate (Hobson 1999, Kelly 2000, Hall-Aspland et al. 2005). The diet of polar bears foraging on the sea ice consists of both lipid-rich blubber and the proteinaceous tissues from their marine mammal prey (Stirling and McEwan 1975, Stirling and Archibald 1977). Therefore, I used stable isotope mixing models to separately estimate protein ($\delta^{13}C$, $\delta^{15}N$) and lipid ($\delta^{13}C$) dietary inputs. I used existing knowledge of the relative lipid and protein intake for polar bears and isotopic information from both macromolecules to estimate overall diet composition. I also tested the hypothesis that high degrees of sexual dimorphism observed in polar bears (Derocher and Wiig 2002, Derocher et al. 2005) may lead to differences in diet composition between sexes. Chapter 3 of my dissertation focused on refining the use of intrinsic tracers to determine important prey items and estimate which prey species contribute to lipid and protein portions of the diet. Due to the relatively short-term nature of this portion of my dissertation, the focus of Chapter 3 was on refining the use of intrinsic tracers to determine important prey. The methods developed in this chapter, and baseline information regarding the composition of polar bear diet in the Beaufort Sea, will contribute to future monitoring and conservation efforts of these two subpopulations.

Chapter 4 of my dissertation examined movement patterns and seasonal fidelity of polar bears in relation to seasonal sea ice dynamics and inter-annual changes in the timing of the sea ice freeze-thaw cycle. For this chapter, I examined movement data collected using satellite-linked telemetry on polar bears in western Hudson Bay. The objective was to establish relationships between phenological processes and the timing of polar bear population-level migrations on and off land. Additionally, I used movement data to monitor trends in the dates polar bears migrate with the hypothesis that recent changes to the timing of break-up and freeze-up (Gagnon and Gough 2005, Stirling and Parkinson 2006, Hochheim and Barber 2010) would correlate with changes in the timing of migration. I also used movement data to test if environmental factors such as the timing of break-up, the rate of ice disappearance during break-up, and the geographic distribution of ice during break-up would affect the degree of fidelity polar bears in western Hudson Bay display to specific on-land refugia.

In Chapter 5, I examined how individual exposure to various environmental factors at a local scale affects the timing of migration in western Hudson Bay polar bears. Chapter 5 differed from Chapter 4 in that it examined environmental variability at local scales and individual responses to sea ice dynamics. Specifically, I tested the hypothesis that environmental factors individual bears are exposed to during break-up affect when they abandon the marine habitat and migrate to shore. I predicted that landscape-scale environmental factors correlated with population-level migration patterns differ from those that influence individual migration behaviour at local scales. I also examined the hypothesis that individual parameters, such as age and reproductive class, affect the timing of migration from marine to terrestrial habitats. In this chapter I used high resolution telemetry data that utilized global positioning system (GPS) technology to examine daily polar bear locations in relation to daily ice conditions extracted from satellite images. Due to the high resolution of the GPS collar data, I was able to examine local relationships between individual polar bear migration behaviour and intra-annual sea ice dynamics. Once established these relationships may be monitored to test for plasticity in polar bear migration behaviour as it relates to long- and short-term sea ice dynamics. Additionally, knowledge regarding the relationship between melting sea ice during annual break-up and the timing of polar bear movement from marine to terrestrial habitats may be an important aspect of establishing informative hypotheses regarding the suitability of future polar bear habitat in various regions of the Arctic.

In Chapter 6, I summarized the results of my dissertation and discussed them within the context of monitoring the ecology of polar bears and changing environmental conditions. In this final chapter I highlighted the contributions of my dissertation in relation to future polar bear management and conservation. Additionally, I offered suggestions for future applications and refinements of the summarized monitoring techniques.

Fig. 1.1. The global distribution of polar bear subpopulations. Subpopulation abbreviations: Viscount Melville Sound (VM), Norwegian Bay (NW), Kane Basin (KB), Lancaster Sound (LS), Baffin Bay (BB), Davis Strait (DS) Southern Hudson Bay (SH), Western Hudson Bay (WH), Foxe Basin (FB), Gulf of Boothia (GB), M'Clintock Channel (MC), Southern Beaufort Sea (SB), and Northern Beaufort Sea (NB) (source IUCN Polar Bear Specialist Group, 2006).

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Chapter 2[*]

Fasting physiology of polar bears in relation to environmental change and breeding behavior in the Beaufort Sea

2.1 Introduction

Understanding how environmental variability influences the population dynamics of a species is an integral component of conservation biology. However, measuring the effects of environmental variability on upper trophic level species is difficult due to time lags in population responses (Veit et al. 1997, Thompson and Ollason 2001, Weimerskirch et al. 2003) and the complexity involved in community structure (Hunter and Price 1992, Walther et al. 2002, Lee and Whitledge 2005). Predator management and conservation decisions are commonly based on population estimates but the underlying ecological factors influencing their population trends are often poorly understood. Nevertheless, conservation and monitoring programs focusing on apex predators are ecologically important because predator density is dependent on total ecosystem productivity (Hooker and Gerber 2004, Sergio et al. 2006). Developing methods to monitor the physiological responses of top predators to environmental change is one way to improve our understanding of factors involved in predator population fluctuations (Thompson et al. 1997, Wasser et al. 1997).

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The sea ice of the Arctic has shown large-scale changes in response to climate warming. The Arctic ice-ocean system has been warming faster than global averages since the 1960s (Zhang 2005). Recent evidence from passive microwave satellite data collected between 1979-2006 shows significant declines in summer minimum and winter maximum Arctic sea ice extents (Comiso 2006, Stroeve et al. 2006, Serreze et al. 2007). In 2005-2006, mean surface temperatures over the Arctic ice cover were significantly higher than normal (Comiso 2006) and spring melt seasons between 2000-2005 began an average of 13 days earlier when compared to 1980-1989 (Stroeve et al. 2006). It has been hypothesized that such decreases in sea ice extent will affect pagophilic (ice-dependent) marine mammals throughout the Arctic (Stirling and Derocher 1993, Tynan and DeMaster 1997, Derocher et al. 2004). Continued long-term increases in global atmospheric temperatures will result in permanent habitat loss and fragmentation for several of these species (Laidre et al. 2008, Ragen et al. 2008). The polar bear (*Ursus maritimus*) is the apex predator in ice-covered Arctic seas and feeds primarily on ringed seals (*Phoca hispida*) and to a lesser extent bearded seals (*Erignathus barbatus*) (Stirling and McEwan 1975, Stirling and Archibald 1977a, Smith 1980). Earlier break-up in spring and longer ice-free periods have been linked to decreases in body condition and survival of polar bears in the southernmost part of their range, Hudson Bay (Stirling et al. 1999, Obbard et al. 2006, Regehr et al. 2007a).

The Beaufort Sea is one of several seas between the coast surrounding the Arctic Ocean and the permanent pack of the polar basin. This area has two populations of polar bears, the Northern Beaufort Sea and Southern Beaufort Sea (Aars et al. 2006). Although there have been many recent changes to Arctic climate and sea ice composition, direct effects of climate change on polar bears in the Beaufort Sea have not been well established. However, a number of recent observations in the Southern Beaufort Sea have been consistent with predictions regarding possible climate-induced stresses on polar bears. Unusual ice conditions and strong winds were linked to a drowning event where up to 27 polar bears were thought to have died (Monnett and Gleason 2006). Further, a report of polar bears showing unusual and energetically inefficient foraging behaviors suggests that Southern Beaufort Sea bears were food-stressed in recent years (Stirling et al. 2008a). A number of cannibalism events were also thought to be related to bears having difficulty obtaining food (Amstrup et al. 2006, Stirling et al. 2008a). Significant reductions in population size estimates have not been reported for either the Northern or Southern Beaufort Sea populations, but decreases in cub-of-the-year survival and recruitment indicate the Southern Beaufort Sea population may currently be declining (Regehr et al. 2006, Rode et al. 2007, Stirling et al. 2007). Regehr et al. (2007b) suggest that increases in the duration of ice-free periods over the continental shelf have been associated with decreases in survival and reproduction for Southern Beaufort Sea polar bears.

Even though polar bears are adept swimmers, they are dependent upon sea ice as a platform from which to hunt seals (Stirling and Derocher 1993, Ferguson et al. 2000a, Derocher et al. 2004). With the exception of pregnant females, most of which over-winter in dens on land, the majority of polar bears in the Beaufort

Sea stay on the sea ice throughout the year (Amstrup et al. 2000, Stirling 2002, Fischbach et al. 2007). During winter and spring, the bears reside on sea ice over the continental shelf where seal densities are higher than farther offshore (Stirling and Archibald 1977b, Stirling et al. 1982). The Beaufort Sea continental shelf region is typically ice-free in late summer and bears are forced farther offshore onto multiyear ice that occurs over deeper and less productive waters (Pomeroy 1997, Lee and Whitledge 2005). In recent years, some Beaufort Sea polar bears have also been observed spending the late summer months on land (Schliebe et al. 2008). Regardless of where the bears go when the sea ice retreats north, they must obtain sufficient fat reserves during spring to get them through summer when prey is less available.

Despite recent anecdotal observations of nutritional stress among polar bears in the Southern Beaufort Sea (Amstrup et al. 2006, Stirling et al. 2008a), no quantitative data exist regarding the feeding frequency and hunting success of bears in the region. However, blood samples collected during routine spring mark and recapture studies can be used to assess feeding status over time by measuring serum urea to creatinine ratios (U/C) (Nelson et al. 1983, 1984, Derocher et al. 1990, Ramsay et al. 1991). Polar bear U/C values decline markedly when they are in a biochemical fasting state, which involves the recycling of nitrogenous wastes into amino acids, minimizing the loss of lean muscle tissue (Nelson 1987). This physiological fasting state is similar to winter dormancy in black bears (*U. americanus*) and grizzly bears (*U. arctos*) (Nelson et al. 1983, Nelson 1987, Derocher et al. 1990). However, polar bears are able to enter this state while active and at any time of the year, provided they have sufficient endogenous fat reserves (Derocher et al. 1990, Ramsay et al. 1991, Ferguson et al. 2000b). In rare cases when mammals completely deplete their fat stores and do not have access to food they may increase protein catabolism in skeletal and cardiac muscles resulting in elevated U/C values (Ramsay et al. 1991, Mustonen et al. 2006). However, in fasting-adapted species this only occurs when individuals are experiencing advanced stages of starvation which ultimately results in vital organ failure and death (Castellini and Rea 1992, Cattet 2000, Mustonen et al. 2006). Polar bears in this situation are rarely observed in the wild and can be identified through routine assessments of the amount of subcutaneous fat present on the body (Stirling et al. 2008b) and obvious behavioral abnormalities.

In this study I compared the serum U/C values in polar bears captured during April-May in 1985, 1986, 2005, and 2006 from the Northern and Southern Beaufort Sea populations. I tested the hypothesis that polar bear feeding success differed in response to climate-induced changes in sea ice conditions in the Beaufort Sea throughout the study period. In addition, I examined the relationship between the frequency of fasting in a given year and estimated body masses. I also tested whether the proportion of bears fasting differed between the two populations to determine if there were any broad-scale geographic differences in feeding. Finally, I compared fasting frequencies among bears differing in sex, age, and reproductive status. It has been hypothesized that adult male polar bears may enter a fasting state during the breeding season because courting behavior reduces the time available for hunting (Ramsay et al. 1991). Because my samples were collected during the breeding season it is expected that adult males may display a higher frequency of fasting than other sex, age, and reproductive classes.

2.2 Materials and Methods

The study area included the offshore regions of the south-eastern Beaufort Sea along the mainland coast between the Alaska/Yukon and Northwest Territories/Nunavut borders, Amundsen Gulf, and offshore of the west coast of Banks Island (Fig. 2.1). Polar bears were located by helicopter and anesthetized with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®) using standard immobilization techniques (Stirling et al. 1989). A vestigial premolar was extracted from each bear for age determination (Calvert and Ramsay 1998). Axillary girth (AG) measurements were taken around the chest of the bear behind the forelegs using a nylon rope tightened with approximately 1 kg of pressure. Straight-line body length (BL) was measured from the tip of the nose to the end of the last tail vertebra. Blood was drawn from a femoral vein and stored in a cooler until it was centrifuged to separate serum and cellular portions. Serum was stored frozen until analysis. Serum urea nitrogen and serum creatinine concentrations were determined for the 1985-1986 samples at the College of Medicine, University of Illinois (Chicago, IL, USA) and for the 2005-2006 samples at Central Laboratory for Veterinarians (Langley, BC, Canada). Serum urea creatinine ratios (U/C) were calculated as (urea nitrogen/0.466)/creatinine (Nelson et al. 1984). Bears with U/C values ≤ 10.0 were considered to be in a physiological fasting state based on Nelson et al. (1984). Research on polar bears in western Hudson Bay indicates that longer fasting periods result in a higher proportion of bears with U/C values in this range (Ramsay et al. 1991), and experimental fasting trials suggest that fasts > 1 week are required to attain U/C values ≤ 10.0 (Derocher et al. 1990).

Statistical analyses were performed using SPSS statistical software (SPSS Inc., Chicago, IL, USA). Both forward and backward stepwise logistic regressions were used to evaluate factors identified as potentially important to the binary response variable fasting or not fasting. Entry testing for forward stepwise regression was based on the significance ($p < 0.05$) of Rao's efficient score statistics. Removal testing for forward and backward stepwise regression techniques was based on the significance ($p < 0.10$) of the Wald's statistic. All independent variables were tested for multicollinearity by placing them into an equivalent ordinary least squares regression and examining their variance inflation factor (Allison 1999). Explanatory variables considered in the model were: class (adult males, adult males accompanying an estrous female, adult females, adult females with cubs, and subadults), population, and capture year. The interactions between class and capture year, and population and capture year were also tested.

Adults were defined as individuals ≥ 5 years of age. Females with cubs were defined as individuals accompanied by cubs-of-the-year, 1-, or 2-year-old cubs. Bears 3 or 4 years old were classed as subadults. Solitary 2 year olds were excluded from analyses because the timing of separation from their mother was unknown. Each individual was assigned to the population where their capture was located using boundaries defined by the IUCN/SSC Polar Bear Specialist Group (Fig. 2.1) (Aars et al. 2006). Polar bear captures occurred during April and May each year, but the dates of capture varied somewhat among years. Because I was concerned that differences in capture period among years might bias my fasting data, I removed 28 outliers by excluding captures occurring on days that did not overlap with capture dates from any other year.

I converted U/C values into a binary response variable of fasting or not fasting based on Nelson et al. (1984). However, Ramsay et al. (1991) found a correlation between mean U/C values and feeding opportunity, so in addition to analyzing the binary response variable I also compared mean U/C values among capture years. U/C values were log-transformed to improve normality and the log-transformed values were compared among years using an ANOVA and post-hoc Tukey-Kramer multiple comparisons of means. I also tested for yearly differences in the estimated body mass of captured polar bears to assess possible changes in body condition. Body mass (M) for each bear was estimated using AG and BL and the multiple regression equation $M = 0.00003377 * AG^{1.7515} * BL^{1.3678}$ (Derocher and Wiig 2002). The mass estimation equation developed for Beaufort Sea bears (Durner and Amstrup 1996) could not be applied because of methodological differences in measuring BL. I calculated the deviances of estimated masses from male and female specific von Bertalanffy curves fitted to age and body mass (Derocher and Wiig 2002). Each deviance measurement was calculated as a proportion of its corresponding von Bertalanffy curve value. The

Kruskal-Wallis test was used to compare the proportional deviances among years for males and females separately.

2.3 Results

Sampling effort was divided relatively evenly between the populations within each year (Fig. 2.1). Mean capture dates occurred on April 25 in 1985, April 29 in 1986, April 22 in 2005, and April 22 in 2006. The number of individuals resampled once or more among years was small, ranging from 0 - 13 individuals for a given year, so each sample was considered independent. I sampled 83, 133, 145, and 75 individual polar bears in 1985, 1986, 2005, and 2006, respectively (Table 2.1). None of the bears displayed physical or behavioral traits indicative of an animal in the advanced stages of starvation. The percentage of all polar bears captured that were in a fasting state was 9.6% in 1985, 10.5% in 1986, 21.4% in 2005, and 29.3% in 2006 (Fig. 2.2).

Forward and backward stepwise logistic regression techniques produced an identical significant model (Model $\chi^2 = 28.90$, d.f. = 7, $p < 0.001$). The model showed that solitary adult males (Wald $\chi^2 = 4.24$, d.f. = 1, $p = 0.039$), adult males accompanying an estrous female (Wald $\chi^2 = 8.06$, d.f. = 1, $p = 0.005$), and the 2005 (Wald $\chi^2 = 4.27$, d.f. = 1, $p = 0.039$) and 2006 (Wald $\chi^2 = 8.18$, d.f. = 1, $p = 0.004$) capture years were significant predictors of polar bear fasting (Table 2.2, Fig. 2.3). When the independent variables were placed in an equivalent ordinary least squares regression their variance inflation factors were 1.02 for both population and class, and 1.03 for capture year. Allison (1999) suggests that multicollinearity is not an issue when the variance inflation factor is < 10, which was the case for all of my independent variables.

There was a significant difference in U/C means among capture years (ANOVA, log-transformed, $F_{3,432} = 4.99$, *p* = 0.002). A post-hoc Tukey-Kramer multiple comparison of means showed the log-transformed U/C values in 2006 were lower than 1985 (*p* = 0.046) and 1986 (*p* = 0.007). The 2005 log-transformed U/C values did not differ from 1985 (*p* = 0.17) but were lower than those in 1986 (*p* = 0.031). There was no difference between the log-transformed U/C values in 1985 and 1986 (*p* = 0.98) or 2005 and 2006 (*p* = 0.78). There were no yearly differences in proportional deviations from the von Bertalanffy curves fitted to age and body mass for males (Kruskal-Wallis: $\chi^2 = 0.97$, d.f. = 3, *p* = 0.81) or females (Kruskal-Wallis: $\chi^2 = 1.72$, d.f. = 3, *p* = 0.63).

2.4 Discussion

Physiological studies are becoming increasingly important in conservation biology and can help determine how animals respond to environmental change (Walker et al. 2005, Carey 2005, Wikelski and Cooke 2006). Numerous blood parameters have been used to monitor wildlife health and nutritional status with varying degrees of success (e.g., Seiser et al. 2000, Golet et al. 2002, Bowyer et al. 2003, Trites and Donnelly 2003, Sanchez-Guzman et al. 2004). In my study, serum U/C values were used as a specific blood biomarker to monitor fasting by polar bears in the Beaufort Sea. My results indicate that polar bears from all sex, age, and reproductive classes in 2005-2006 were more likely to be in a physiological fasting state than in 1985-1986. Adult males from all years of the study, especially those engaged in breeding activity at the time of capture, were also more likely to be fasting than bears in other sex, age, and reproductive classes. Population was not a significant predictor variable of fasting during any year, indicating that feeding opportunity was similar in the Northern versus Southern Beaufort Sea.

The observed increase in bears fasting during 2005-2006 is consistent with other reports which provide evidence that polar bears in the Beaufort Sea may have been food-stressed in recent years (Amstrup et al. 2006, Rode et al. 2007, Stirling et al. 2008a). Beaufort Sea bears reach their lightest weights in late March and rely on a 2-3 month spring feeding period, when fat and naive ringed seal pups are available, to gain the fat reserves necessary for survival and reproduction (Stirling and Øritsland 1995, Stirling 2002). Because polar bears are typically in a hyperphagic state during the spring (Ramsay and Stirling 1988, Derocher and Taylor 1994), the recent increase in bears fasting during April and May suggests that there has been a decrease in prey availability at that time of year. Although there have been large-scale changes in sea ice extent and condition throughout the Arctic Ocean (Comiso 2006, Stroeve et al. 2006, Serreze et al. 2007), the precise means through which prey have apparently become less available to polar bears in the Beaufort Sea remains unknown. It is possible that changes to ice composition have made hunting conditions less favorable and thus diminished hunting success. Stirling et al. (2008a) propose that wide expanses of open water during winter in 2005-2006, combined with intense wind storms, created extensive rubble fields of thick ice making it difficult for polar bears in the southern Beaufort Sea to access ringed seal lairs. Changes to sea ice composition during the spring or other times of the year could also affect ringed seal abundance. Information on seal densities in the Beaufort Sea is lacking; however, warmer spring temperatures and earlier spring breakup can affect ringed seal pup development and survival (Harwood et al. 2000, Smith and Harwood 2001, Ferguson et al. 2005). Any environmental changes affecting local ringed seal population dynamics are likely to influence the amount of food available for polar bears.

The higher proportion of adult males fasting could be attributed to spring breeding behavior which was supported by the logistic regression model where adult males accompanied by an estrous female were stronger predictors of fasting than solitary adult males. Breeding activity for polar bears occurs from March through June (Lønø 1970, Rosing-Asvid et al. 2002, Amstrup 2003). During this time, males search for estrous females and likely consume less food (Ramsay and Stirling 1986, Ramsay et al. 1991, Stirling et al. 1993). In support of this, Ramsay et al. (1991) reported that males consorting with females during the spring had significantly lower mean U/C values than solitary males. Similarly, reduced foraging by males during the mating season has been observed in black bears (Herrero 1983, Rogers 1987) and several species of seals (Anderson and Fedak 1985, Le Boeuf and Laws 1994, Coltman et al. 1997). My results support the hypothesis that adult males eat less frequently during the breeding season, presumably because the need to find and maintain access to mates prevents effective hunting. The increased proportion of bears fasting in 2005-2006 could partially be due to more males breeding as recent declines in cub-of-the-year survival and recruitment (Regehr et al. 2006, Rode et al. 2007) would result in a higher number of available estrous females.

Decreased food availability has been shown to coincide with decreases in average U/C values (Ramsay et al. 1991, Tryland et al. 2002). The results of my U/C value comparisons correspond with the conclusions of my logistic regression, with the exception of the lack of a significant difference between 1985 and 2005. However, comparisons of mean U/C values are likely less reliable than comparisons using a binary fasting/non-fasting classification due to the wide distribution of values occurring above 10. For instance, U/C values in Beaufort Sea polar bears ranged from 2.0 - 138.9. U/C values ≤ 10 indicate fasting in black bears (Nelson et al. 1984), and studies on polar bears found that fasting individuals also had values in this range (Lee et al. 1977, Nelson et al. 1983, Ramsay et al. 1991). However, the factors responsible for the wide range of U/C values above 10 are unclear. Serum U/C in bears may be dependent on a number of factors including renal function, protein intake, and protein catabolism (Lee et al. 1977, Hellgren et al. 1990, Atkinson et al. 1996, Lohuis et al. 2005). Many of these cannot be measured in the field and therefore comparisons of mean U/C values should be interpreted cautiously. Carefully designed studies on feeding and fasting captive polar bears would be useful to evaluate factors influencing U/C values > 10.0.

An increase in the number of polar bears fasting would be expected to correspond with a decrease in body condition. However, even though the incidence of fasting was greater in 2005-2006, there was no detectable difference in estimated body mass among years. Polar bear body mass is dependent upon age and sex (Kingsley 1979, Derocher and Wiig 2002, Derocher et al. 2005) and caution must be used when comparing estimated masses among years. Even if body mass comparisons are done separately for each sex, the distribution of ages within a given year can introduce bias. To overcome this difficulty I compared deviances of estimated masses from male and female specific von Bertalanffy curves fitted to age and body mass (Derocher and Wiig 2002). However, the relationships used to determine mass estimate equations may not remain constant over time and this could have affected my ability to detect changes in body mass (Cattet and Obbard 2005). In addition, increases in the proportion of bears fasting in 2005-2006 relative to 1985-1986 may not have been great enough to cause overall declines in estimated body mass. Data collected between 1971-1994 indicates that ringed seal pup production in the Beaufort Sea was low during the mid 1980s, and coinciding decreases in polar bear natality were observed (Stirling 2002). Thus, polar bears captured during 1985-1986 were likely in poor body condition relative to years of higher ringed seal production. The increased proportion of individuals fasting in recent years may indicate that polar bears are having even more difficulty obtaining food than in the mid 1980s. Incorporating serum U/C measurements into long-term monitoring programs could prove useful in providing early indications of nutritional stress that may not be detectable in population level body mass comparisons.

This study was designed to examine variation in the spring feeding ecology of polar bears during two distinct time frames. However, logistical constraints involving weather, local sea ice, and tracking conditions prevented the occurance of captures on precisely consistent days each year. Differences in mean capture dates occurring among some of the years could confound the observed year effect in polar bear fasting. However, differences that occurred in mean capture dates were only 3-7 days and all of my capture periods had a high degree of overlap. Given that ringed seal pups are born throughout March and April (Stirling and McEwan 1975, Smith and Stirling 1975) it is unlikely that differences in mean capture dates ≤ 1 week would bias my results.

Serum U/C values are a useful physiological biomarker that can be used to monitor long-term patterns in polar bear feeding ecology. The increased proportion of individuals fasting in recent years is consistent with other observations regarding the feeding ecology of polar bears in the Beaufort Sea (Amstrup et al. 2006, Stirling et al. 2008a). Whether the apparent decrease in polar bear feeding is a short-term occurrence or an indicator of future conditions is unknown. Like all bear species, polar bears are long-lived animals with low reproductive rates (Bunnell and Tait 1981, Ramsay and Stirling 1988) and it is likely that population fluctuations lag behind environmental changes. Understanding the proximate mechanisms involved in population fluctuations and how they relate to environmental stressors, such as climate change, may provide timely indicators of future demographic responses.

Table 2.1 Sample sizes and mean serum urea/creatinine (U/C) values for polar bears caught in the Northern Beaufort Sea and Southern Beaufort Sea populations for 1985-86 and 2005-06.

Year	Class	n	Mean U/C +/- SE	U/C Range
1985 n = 83	Solitary adult males	23	33.3 +/- 2.6	5.1 - 109.7
	Adult males with estrous female	3		
	Adult females	15		
	Females with cubs	14		
	Subadults	28		
1986 N = 133	Solitary adult males	36	37.0 +/- 2.5	4.2 - 138.9
	Adult males with estrous female	10		
	Adult females	34		
	Females with cubs	23		
	Subadults	30		
2005 N = 145	Solitary adult males	39	30.4 +/- 2.2	2.0 - 137.4
	Adult males with estrous female	10		
	Adult females	40		
	Females with cubs	28		
	Subadults	28		
2006 n = 75	Solitary adult males	21	26.1 +/- 2.5	4.1 - 91.4
	Adult males with estrous female	3		
	Adult females	23		
	Females with cubs	21		
	Subadults	7		

Table 2.2 Variables and their corresponding parameter estimates for the final logistic regression model predicting fasting in polar bears (n = 436) from the Beaufort Sea. Non-significant factors (population, class*capture year, and population*capture year) are not shown.

Predictor Variable	**β**	**S.E.**	**Wald's Statistic**	***P***	**Exp (β)**
Class*					
Solitary adult males	0.76	0.37	4.24	0.039	2.14
Adult males with estrous female	1.47	0.52	8.06	0.005	4.35
Females with cubs	0.54	0.40	1.80	0.180	1.71
Subadults	-0.06	0.46	0.016	0.901	0.94
Capture year*					
1986	0.02	0.47	0.002	0.961	1.02
2005	0.89	0.43	4.27	0.039	2.44
2006	1.32	0.46	8.18	0.004	3.74
Constant	-1.55	0.16	98.96	<0.001	0.21

*References for class and capture year are adult females and 1985 respectively.

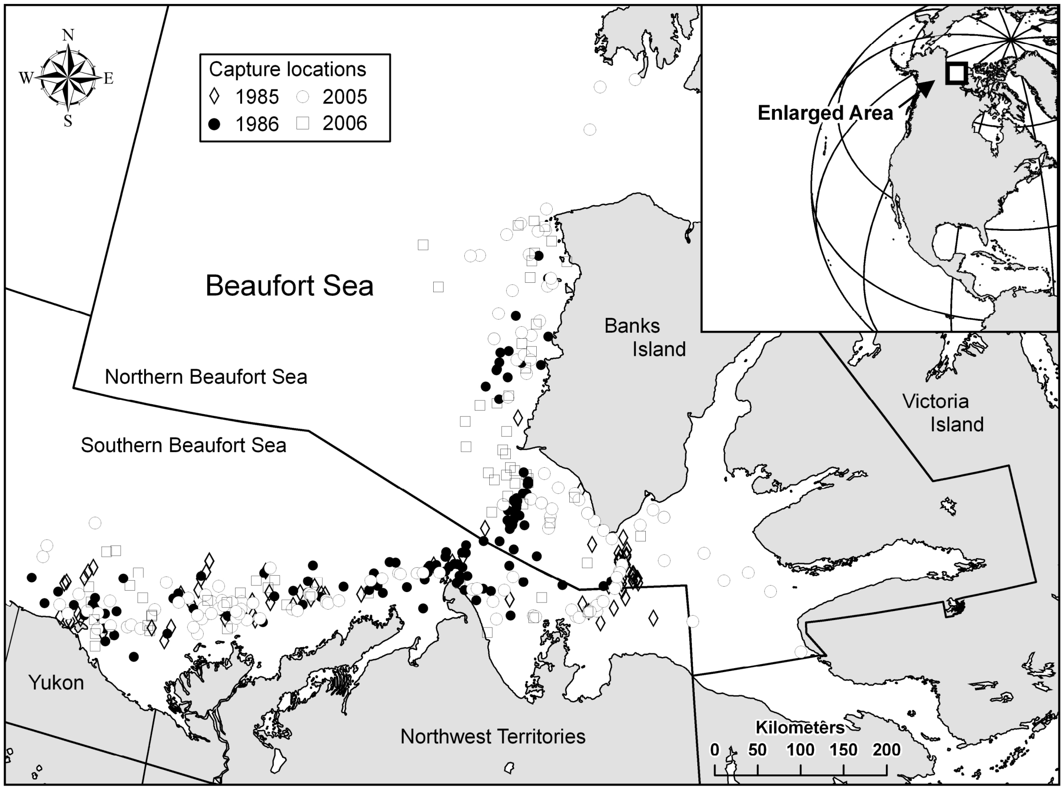

Fig. 2.1 Map of study site and capture locations of polar bears in the Northern Beaufort Sea and Southern Beaufort Sea subpopulations.

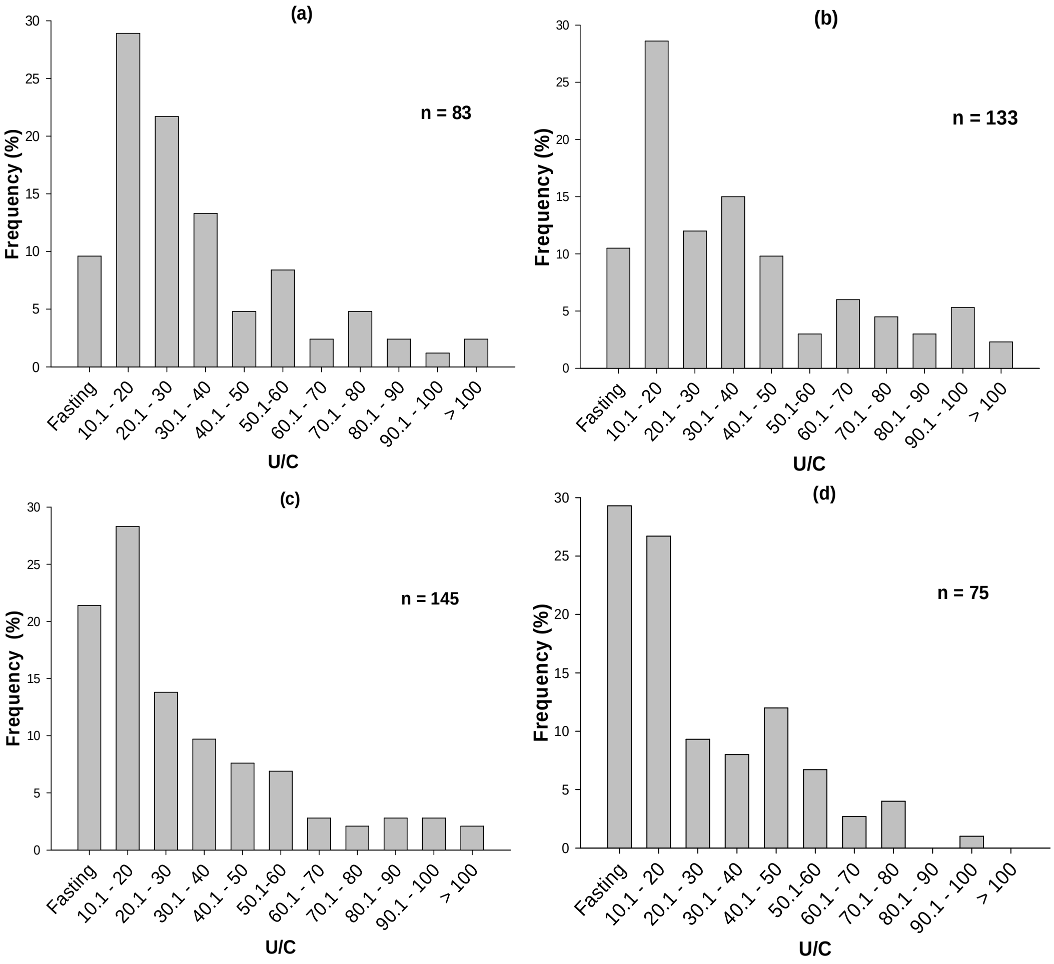

Fig. 2.2 Frequency distribution of serum urea/creatinine (U/C) values for polar bears captured in the Northern Beaufort Sea and Southern Beaufort Sea during spring in (a) 1985, (b) 1986, (c) 2005, and (d) 2006. Fasting individuals were defined as those with U/C values ≤ 10.0 following Nelson et al. (1984).

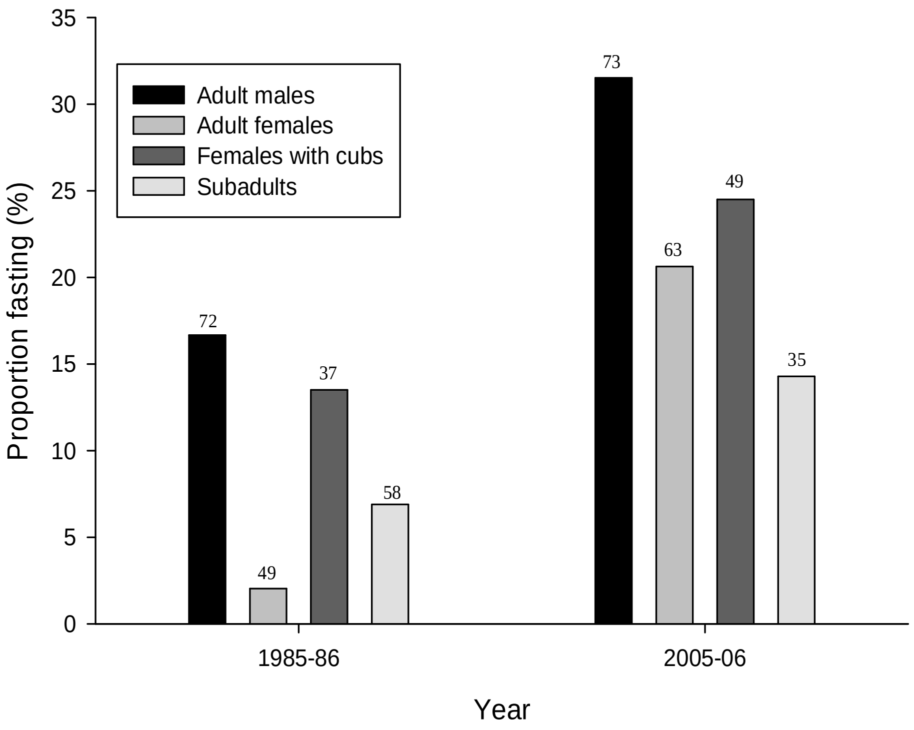

Fig. 2.3 Proportion of polar bears fasting in each class during April and May in the Beaufort Sea. The adult male class represents both solitary individuals and adult males that were accompanied by a female at the time of capture. Numbers above the bars indicate sample size. Data were pooled among capture periods that were significant predictors in the logistic regression model (2005-06) and separately for capture periods that were not significant (1985-86).

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Chapter 3[*]

Quantifying dietary pathways of proteins and lipids to tissues of a marine predator

3.1 Introduction

Conventional methods of investigating animal diets have included the examination of stomach contents, faecal analysis, and direct observation of feeding. Because of biases and limitations associated with each of these methods (Reynolds and Aebischer 1991, Spaulding et al. 2000, Redpath et al. 2001), researchers have increasingly employed measurements of naturally occurring endogenous tracers such as stable isotopes. Stable isotope techniques have been used to reconstruct both paleo and contemporary diets of a variety of species (West et al. 2006, Fox-Dobbs et al. 2008) and also to examine food web structure, niche breadth, and contaminant pathways (Newsome et al. 2007, Schmidt et al. 2007, Cardona-Marek et al. 2009). The application of stable isotope methods to estimate dietary contributions or trophic level is possible because consumer tissue isotope values reflect those in their diet and thus act as ecological tracers throughout the food web (Deniro and Epstein 1978, 1981, Tieszen and Boutton 1989). Diet reconstruction using stable isotopes is advantageous because it allows evaluation of assimilated nutrients over ecologically relevant time-scales rather than just recently ingested items (Tieszen et al. 1983, Hobson and Clark 1992).

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The ability to examine previously assimilated nutrients from tissue samples is particularly useful for monitoring wide-ranging or migratory species whose diets would otherwise be logistically difficult and costly to evaluate for extended time periods. Stable isotope analysis is therefore a useful technique for examining the diet of highly mobile marine predators such as polar bears (*Ursus maritimus*).

The diet of polar bears inhabiting the Arctic sea ice is primarily composed of marine mammals and consists of blubber augmented with muscle and other proteinaceous tissues such as skin and viscera (Lønø 1970, Stirling and McEwan 1975, Stirling and Archibald 1977). Blubber in marine mammals is principally composed of lipid and contains little protein, whereas muscle tissue is a significant source of protein but contains limited amounts of lipid (Best 1985, Beck et al. 1993, Gales et al. 1994). Within a bear, protein and lipid may be differentially routed because it is metabolically more efficient to utilize dietary lipid for endogenous lipid stores and energy, and dietary proteins for body protein synthesis (Pond 1981, Hobson and Bairlein 2003, Wortinger 2007). Therefore, stable isotope diet studies should consider that isotopes from different dietary components are not distributed uniformly among a bear's tissues (Schwarcz 1991, Phillips and Koch 2002, Martinez del Rio et al. 2009). As a result, polar bear tissues may not reflect isotopic composition of the overall diet, but rather the composition of specific dietary macromolecules preferentially used to synthesize a given tissue type (Gannes et al. 1997, Hobson and Stirling 1997, Podlesak and McWilliams 2006, Voigt et al. 2008, Hobson et al. 2009).

Stable isotope diet studies have typically used proteinaceous tissues with lipids removed to represent the diet of polar bears as a wholly carnivorous diet of marine mammal muscle and blubber (Bentzen et al. 2007, 2008). However, using such a protein-metabolic pathway to draw inferences regarding the overall diet of a consumer is only valid if the proportion of protein to lipid consumed is the same from all prey sources. Best (1985) reports that two captive polar bears given the opportunity to regulate their consumption of muscle and blubber over a five-month period consumed approximately 20% muscle and 80% blubber. These estimates for protein intake are similar to the long-term protein requirements for the closely related grizzly bear *U. arctos* (Felicetti et al. 2003). However, even though bears regulate their protein intake to meet, but not exceed, physiological requirements over long time periods (Robbins et al. 2007), the ratio of lipid to protein consumed by polar bears during each feeding event may depend on prey type and size. Polar bears preferentially consume the blubber portion of a carcass (Stirling 1974, Stirling and McEwan 1975, Stirling and Archibald 1977) and large prey often consist of enough blubber to satiate a polar bear. In addition, the intake of protein versus lipid during scavenging events will depend on how much of a carcass remains, which may also be related to prey type and size.

Polar bears in the Beaufort Sea have access to four species of marine mammal prey: ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*), beluga whales (*Delphinapterus leucas*), and bowhead whales (*Balaena mysticetus*). However, consumption of bowhead and most consumption of beluga whales is through scavenging. I hypothesized polar bears would consume proportionately more lipid when eating large prey such as bearded seals, beluga whales, and bowhead whales and conversely, would consume proportionately more protein from small prey (i.e. ringed seals, Fig. 3.1). To test this hypothesis, I separately analyzed and compared the isotopic composition of dietary protein and lipid by using both proteinaceous and lipid tissue samples. I predicted that isotopic diet reconstruction using proteinaceous tissues would indicate a greater consumption of small prey than would methods utilizing lipid tissues. Current estimates of the approximate consumption of protein and lipid by polar bears were then used to combine mixing model source estimates for each tissue type to determine polar bear diet. Combined models incorporating both protein and lipid metabolic pathways were compared with those using the more orthodox approach of analyzing proteinaceous tissues only.

3.2 Materials and Methods

Collection of polar bear and prey tissues

Adult polar bears (≥5yrs; 21 male, 26 female) were captured on sea ice over the continental shelf in the southern Beaufort Sea (Fig. 3.2). Bears were located using a helicopter and immobilized via remote injection (Stirling et al. 1989). All polar bear captures occurred between 6 April and 9 May 2005. Animal handling procedures were approved by the University of Alberta Biological Sciences Animal Policy and Welfare Committee. Blood was drawn from the femoral vein into sterile Vacutainer® tubes with no additives. Adipose tissue samples were collected from the rump of each bear using 8 mm biopsy punches. A vestigial premolar removed at capture was used to determine age (Calvert and Ramsay 1998). Muscle and blubber samples were collected from potential prey species of polar bears throughout the Beaufort Sea from 2003–2007 (Table 3.1). Ringed seal and bearded seal samples were collected opportunistically from the remains of seals that had been killed by polar bears. Beluga and bowhead whale tissues were sampled from Inuit community-based harvests throughout the southern Beaufort Sea.

Stable isotope analysis

Muscle from prey and whole blood from polar bears were freeze-dried and then soaked in a 2:1 chloroform:methanol solution to remove lipids prior to analysis. Adipose tissue samples from polar bears and blubber from prey were soaked in the same solvent mixture to obtain lipids for isotope analysis (Bond et al. 2007). Muscle and blood samples were homogenized into a powder with a mortar and pestle. Approximately 1 mg of each muscle and blood sample and 0.6 mg of each lipid sample were weighed into tin capsules and combusted in a Europa 20:20 continuous-flow isotope-ratio mass spectrometer (Department of Soil Sciences, University of Saskatchewan). Laboratory standards of whale baleen (BWB II) and egg albumen were analyzed for every five unknowns. Based on standard deviations of within-run replicate measurements of standards, analytical error was estimated to be ± 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$ measurements. Stable isotope values are presented in the standard δ-notation as parts per thousand (‰) relative to Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric air ($\delta^{15}N$) standards.

Statistical analyses and isotope mixing models

I used stable isotope mixing models to estimate the contribution of carbon and nitrogen from various prey to polar bear tissues. For n isotopes and $> n+1$ possible dietary sources, no unique solution is possible (Phillips and Gregg 2003, Moore and Semmens 2008). However, probability based models are available to constrain the range of potential prey inputs in these cases. I used MixSIR (version 1.04), a stable isotope source-partitioning mixing model that utilizes a Bayesian framework to estimate the probability distributions of the proportional contribution for each possible prey source (Moore and Semmens 2008). All my models were run with uninformative priors (Moore and Semmens 2008).

I assessed the relative contribution of each prey source to both the protein- and lipid-metabolic pathways in polar bears by conducting separate stable isotope mixing models for each macromolecule pathway. For protein, mean prey isotope values for lipid-free muscle and associated standard deviations were used as source data and isotope values from lipid-free polar bear whole blood represented the consumer mixture. In the lipid-mixing models, mean isotope values and the associated standard deviations from prey blubber lipid were used as source data and isotope values from polar bear adipose lipid represented the consumer mixture. Because lipid is nitrogen-deficient (Bearhop et al. 2002, Minami and

Nakamura 2005, Camin et al. 2007), only $\delta^{13}C$ values could be used to assess source contributions to the lipid-metabolic pathway.

I constructed and compared single ($\delta^{13}C$) and dual ($\delta^{13}C$ and $\delta^{15}N$) isotope mixing models for the polar bear protein pathway. This comparison was conducted to determine if the inclusion of additional isotope values available in proteinaceous tissues (i.e. $\delta^{15}N$) would confound comparisons between protein- and lipid-based mixing models. Before constructing single isotope mixing models, $\delta^{13}C$ values of male and female polar bears were compared using separate Student's *t*-tests for blood and lipid. When $\delta^{13}C$ values differed significantly in either blood or lipid, males and females were treated as separate consumers and thus each had their own set of mixing models. Similarly, before constructing dual isotope mixing models, a Hotelling's T^2-test was used to compare blood $\delta^{13}C$ and $\delta^{15}N$ values simultaneously between male and female polar bears. Separate mixing models were used when significant differences occurred. These two-isotope protein-based mixing model results were used in combination with source estimates from the lipid-based models to determine the diet of polar bears.

Because the gross composition of polar bear diet was estimated to be 20% muscle and 80% blubber (Best 1985), I multiplied the estimated contributions of each source in the protein- and lipid-metabolic pathways by 0.20 and 0.80, respectively, to estimate the proportions of protein and lipid consumed from each prey relative to total protein and lipid intake. Estimated source contributions from each metabolic pathway were then combined by adding the lower and upper values from the range of feasible solutions for matching sources in each pathway to establish a minimum and maximum contribution for each prey to the overall diet. I was interested in examining the contribution of small prey (ringed seal) relative to large prey (bearded seal, beluga whale, and bowhead whale) in each metabolic pathway, so I aggregated large prey source contributions *a posteriori* to constrain the number of sources in my mixing model results (Phillips et al. 2005). I also performed an *a posteriori* aggregation of large prey on the overall diet estimates for polar bears that combined results from the protein- and lipid-metabolic pathways.

There are no data on diet-tissue isotopic discrimination values for polar bears fed a known diet. However, I extracted values from published data for captive carnivores feeding on known carnivorous diets (i.e. animal flesh) to estimate discrimination factors between prey muscle and polar bear whole blood. I used the mean of 18 carbon and nitrogen red blood cell and serum discrimination factors from a table summarizing published values in Caut et al. (2009). The discrimination values utilized were for marine and terrestrial carnivores, which included black bears *U. americanus*, grizzly bears, and a variety of seal species (Hilderbrand et al. 1996, Hobson et al. 1996, Kurle 2002, Lesage et al. 2002, Felicetti et al. 2003). Values of 1.21‰ (S.D. = 0.85) for $\delta^{13}C$ and 2.75‰ (S.D. = 1.03) for $\delta^{15}N$ were derived and added to isotope values for all prey muscle samples. I assumed no discrimination between prey lipid and polar bear lipid (Gannes et al. 1997, Podlesak and McWilliams 2007, Hobson et al. 2009).

3.3 Results

Male polar bears had higher blood and lipid $\delta^{13}C$ values than females (blood, t = 3.15, d.f. = 45, $P < 0.01$; lipid, t = 3.72, d.f. =45, $P < 0.001$) (Table 3.1); therefore sex-specific $\delta^{13}C$ protein- and lipid-metabolic pathway mixing models were created. When blood $\delta^{13}C$ and $\delta^{15}N$ values of males and females were compared simultaneously, there were also significant differences (Hotelling's T^2: $F_{2,44} = 8.67$, $P < 0.001$) and thus separate two-isotope ($\delta^{13}C$ and $\delta^{15}N$) protein-metabolic pathway mixing models were used for each sex. Sample sizes for prey lipid were often smaller than sample sizes for muscle because virtually all of the blubber had been consumed at many kills (Table 3.1). For all mixing models I present results before and after aggregation of large prey. Source estimates subsequent to aggregating large prey are presented to demonstrate the combination of results from the protein- and lipid-metabolic pathways (Fig. 3.3). The same methods for combining estimates from both metabolic pathways were used on source estimates for all individual prey (summarized in Table 3.2). Source estimates from single isotope ($\delta^{13}C$) protein-mixing models had substantial overlap with estimates from dual isotope ($\delta^{13}C$ and $\delta^{15}N$) protein-mixing models (Table 3.2). Therefore, inclusion of $\delta^{15}N$ in dual-isotope protein models was unlikely to confound comparisons between results from protein- and lipid- metabolic pathways.

For both sexes, results from the protein-metabolic pathway mixing models differed from those of the lipid-metabolic pathway mixing models, indicating that each prey did not contribute equally to both metabolic pathways (Tables 3.2, Fig. 3.2). Protein-based models predicted a higher contribution from ringed seals than lipid-based models, with ringed seals being the highest contributor to the dietary protein intake of both male and female polar bears. Lipid-metabolic pathway mixing models for males predicted a higher contribution of lipid from large prey compared to ringed seals. Source estimates for female lipid intake also tended towards more large prey; however, there was substantial overlap between ringed seal and large prey estimates. Overall diet of males consisted of a greater proportion of prey larger than ringed seals. Estimates for the proportion of ringed seals versus large prey in the overall diet of females overlapped. However, overall dietary source estimates for females tended towards more ringed seals when compared to overall diet estimates for males. Results using previous methods of analyzing only proteinaceous tissues (see ovals in Fig. 3.3 from the protein pathway) tended to overestimate the proportion of small prey and underestimate the amount of large prey. These discrepancies between the protein-only source estimates versus those using combined protein and lipid estimates were greatest for males.

3.4 Discussion

Carnivores consume both lipid and protein from their prey and these macromolecules may be preferentially routed to analogous tissues within their bodies (Ambrose and Norr 1993, Tieszen and Farge 1993). Most studies of predator foraging using stable isotopes generally assume the amount of lipid ingested is either negligible or that the ratio of protein to lipid consumed is equal across prey types. The results of my mixing models indicate that such assumptions may not hold true and support the prediction that dietary protein and lipid are preferentially routed within the predator. Polar bear diet estimates derived from the protein- and lipid-metabolic pathways differed substantially and because results were similar for the single ($\delta^{13}C$) and dual-isotope ($\delta^{13}C$ and $\delta^{15}N$) protein mixing models, the addition of $\delta^{15}N$ measurements to protein-mixing models could not account for this difference. Protein-based models for both sexes of polar bears predicted greater contributions of small-bodied prey (ringed seals) when compared to lipid-based models. Unequal intake of protein and lipid among various types and sizes of prey is likely to be the main cause of differing source estimates between the protein- and lipid-based stable isotope mixing models.

Polar bears are capable of consuming up to 20% of their body mass in a single meal (Best 1977), which in the Beaufort Sea would be approximately 40 kg for adult females and 84 kg for adult males (based on Derocher 1991). The body mass of small prey such as ringed seals allows adult polar bears to consume all edible proteinaceous and lipid tissue in one feeding event (Stirling and McEwan

1975). In contrast to ringed seals, larger prey consist of enough lipid tissue to satiate a polar bear. Adult bearded seals, based on data from a similar sized northern phocid seal, the hooded seal *Cystophora cristata*, would have roughly 80 kg of lipid tissue available for consumption (Kovacs et al. 1996). Beluga or bowhead whales (total body mass of 1500 to 100,000 kg; O'Corry-Crowe 2002, Rugh and Shelden 2002) would also allow bears to become satiated on lipid tissue alone, sometimes for many days in succession.

The availability of young ringed seal pups prior to the onset of sampling polar bear tissues in the spring may also have contributed to the proportionately higher amount of ringed seals in the protein relative to lipid portion of the diet. Ringed seal pups are born throughout late March and April and newborns have relatively small amounts of lipid (Stirling and McEwan 1975, Lydersen et al. 1992, Lydersen and Hammill 1993). Consequently, ringed seal pups probably contribute proportionately more protein to the diet of polar bears relative to other prey items (Fig. 3.1). In contrast, the bearded seal pupping season does not begin until early May (Smith 1981, Watanabe et al. 2009) making it unlikely that polar bear tissues sampled for this study would contain significant amounts of assimilated nutrients from bearded seal pups.

Polar bears in the Beaufort Sea reach their lightest weights in late winter and then rely on a 2 -3 month hyperphagic period, during optimal seal hunting conditions that occur in the spring, to gain adipose reserves necessary to ensure survival through the rest of the year (Stirling and Øritsland 1995, Stirling 2002). Therefore, my adipose biopsies collected in April and May likely represented recently acquired nutrients and not long-term endogenous reserves. Blood samples were also likely to represent recently acquired nutrients because the half-life of red blood cells is about 28 days in captive black bears *Ursus americanus* (Hilderbrand et al. 1996). The specific isotopic turnover of whole blood and adipose tissue in polar bears is unknown. However, laboratory experiments indicate adipose tissue and whole blood have similar isotopic turnover rates in small mammals (Tieszen at al. 1983, MacAvoy et al. 2005). For these reasons, it is reasonable to assume that my polar bear blood and adipose tissue samples were representative of isotopic diet contributions over the same time period.

In contrast to protein intake, consumption of lipid by male polar bears was predominantly from large prey and their overall diet also reflected a higher proportion of large prey compared to adult females. Because diet estimates using fatty acid analysis indicate males eat a higher proportion of bearded seals relative to females (Thiemann et al. 2007, 2008), it is likely that a large portion of their large prey isotopic signal resulted from bearded seals. Polar bears display a high degree of sexual dimorphism with adult females being approximately half the size of adult males (Derocher and Wiig 2002, Derocher et al. 2005). Therefore, it is less likely for females to be able to prey on bearded seals, especially adults (Stirling and Derocher 1990, Thiemann et al. 2008). Estimates of the proportion of small versus large prey for the lipid-metabolic pathway, and consequently the overall diet, of female polar bears were less conclusive than for males due to a high degree of overlap in mixing model source estimates. Nonetheless, it is clear that both small and large prey are important to the overall diet of female polar bears. However, I suggest that much of the large prey consumed by females resulted from scavenging.

Proteins and lipids often serve different nutritional needs in wild animals and their relative importance is expected to vary depending on age, growth, and reproductive stage (Krapu 1981, Beck et al. 2003, Parker et al. 2009). In high latitude marine systems, diets rich in lipids are often of crucial importance to a wide array of taxa as a form of energy and as a means of providing insulation (Young 1976, Prestrud and Nilssen 1992, Harington 2008). The accurate evaluation of which prey provide protein and lipid sources to consumers in these systems is therefore fundamental to understanding their nutritional ecology. The isotope approach presents a relatively new means of quantifying the origins of these two fundamental macromolecules in animal diets. However, failure to consider both protein and lipid contributions to higher-order consumers such as polar bears could result in overestimating the importance of some food sources and underestimating or excluding key nutritional inputs. Thus, conservation biologists interested in using isotope techniques to examine predator-prey relationships and identify food resources for species of conservation concern need to consider which tissues should be sampled to adequately measure the contributions of all dietary macronutrients. My methods should also be considered in light of seasonal changes to dietary macromolecular composition. For example, migratory birds tend to consume lipid-rich diets during stopover feeding events (Blem 1980, Bairlein 1998) and failure to incorporate contributions to the lipid-metabolic pathways during seasonal migrations is likely to result in erroneous diet estimates using stable isotope measurements.

In this study, similarities between source estimates provided by the lipid pathway and those for the overall diet were probably due to the greater weight (80%) I placed on the lipid pathway based on previous studies of bear nutrition. However, in some instances, weights given to each metabolic pathway may need to be altered. For example, subadult bears have higher protein requirements and intakes because they are still growing and their smaller size, combined with their inexperience at hunting, makes them reliant on scavenging the largely proteinaceous remains of kills made by other polar bears (Stirling and McEwan 1975, Derocher et al. 2004). Additionally, an individual's ability to optimize protein and lipid intake may depend upon the availability of various prey species, which fluctuates with seasonal sea ice dynamics (Stirling and McEwan 1975, Derocher et al. 1990, Polischuk, Norstrom and Ramsay 2002). During spring, polar bears are typically in a hyperphagic period (Ramsay and Stirling 1988, Derocher and Taylor 1994); however, at other times of the year when hunting efficiencies are lower, bears may not always be able to maximize lipid intake.

Understanding the diet of upper-level marine mammals is of particular importance for conservation management, examinations of contaminant exposure, and monitoring for shifts to ecosystem structure (Loseto et al. 2009). Climate-induced changes to predator-prey relationships may cause major adjustments to Arctic marine ecosystems (Higdon and Ferguson 2009) and changes in foraging behaviour have already been observed in polar bears (Stirling et al. 2008, Cherry et al. 2009). Effective monitoring of Arctic marine ecosystems will be facilitated by surveying top predators, which will allow wildlife managers to respond in a proactive manner. Intrinsic tracers in the form of stable isotope measurements offer a practical means of monitoring diet composition of polar bears and many other species of conservation concern. However, the results of this study indicate that previous methods of only isotopically analyzing proteinaceous tissues will not accurately estimate the proportion of various prey species to the overall diet of polar bears. The methods I present for combining source estimates from multiple metabolic pathways to more accurately reflect the overall diet have implications for stable isotope practitioners examining diet in any species that gain disproportionate amounts of dietary macromolecules from various food sources. For example, other bears (e.g. Fortin et al. 2007) as well as marine predators such as killer whales *Orcinus orca* and seals consume varying proportions of lipid and protein from different sizes and types of prey (Jefferson et al. 1991, Budge et al. 2002, Herman et al. 2005). In addition, careful consideration should be given to choosing appropriate tissues for stable isotope analysis when examining relationships between diet and contaminant exposure (i.e. Krahn et al. 2007, McHugh et al. 2007, Bentzen et al. 2008). It is inappropriate to use only stable isotope tracers from proteinaceous tissues when making dietary inferences related to trophic level contaminant transfer because many contaminants primarily accumulate in lipid (Jarman et al. 1996, AMAP 2002, Gray 2002) and because I have demonstrated a decoupling of the protein- and lipid-metabolic pathways. However, separately analyzing and then combining contributions to individual metabolic pathways requires reasonable estimates of the proportion of various macromolecules in the overall diet. In addition to field-based investigations, feeding experiments with captive animals aimed at measuring the consumption of various macromolecules in simulated ecological and physiological scenarios are required to refine the use of isotopic tracers for diet reconstruction.

Table 3.1. The mean $\delta^{13}C$ and $\delta^{15}N$ values of tissues collected from adult male and female polar bears and potential prey sources in the Beaufort Sea, 2003-2007.

Species	**Tissue**	***n***	**Mean $\delta^{13}C$ (‰) ± SE**	**Mean $\delta^{15}N$ (‰) ± SE**
Ringed seal	Muscle	45	-20.6 ± 0.1	18.3 ± 0.2
	Blubber	34	-27.0 ± 0.1	
Bearded seal	Muscle	10	-17.8 ± 0.4	16.8 ± 0.3
	Blubber	7	-25.5 ± 0.5	
Beluga whale	Muscle	11	-18.1 ± 0.1	17.7 ± 0.2
	Blubber	10	-24.4 ± 0.1	
Bowhead whale	Muscle	3	-19.2 ± 0.2	14.3 ± 0.6
	Blubber	3	-26.1 ± 0.6	
Polar bear (male)	Whole blood	21	-19.3 ± 0.1	20.3 ± 0.1
	Adipose	21	-25.7 ± 0.1	
Polar bear (female)	Whole blood	26	-19.6 ± 0.1	20.6 ± 0.1
	Adipose	26	-26.2 ± 0.1	

Table 3.2. The estimated contribution of potential prey to the protein- and lipid-metabolic pathways of female and male polar bears in the Beaufort Sea. The results shown are prior to combining all large-bodied prey and represent 5th to 95th percentiles of MixSIR estimates.

* Contributions to the protein-metabolic pathway (two-isotope models only) were adjusted to amount to 20% of the overall diet, whereas contributions to the lipid-metabolic pathway were adjusted to amount to 80% (based on Best 1985).

Polar bear sex	Prey source	Metabolic pathway	Isotope(s)	Contribution (%) to each pathway	Contribution to Overall Diet (weighted by pathway*)(%)	Total Contribution (%)
Female	Ringed seal	Protein	$\delta^{13}C$	75 – 93		33 – 70
		Protein	$\delta^{13}C$, $\delta^{15}N$	73 – 88	15 – 18	
		Lipid	$\delta^{13}C$	22 – 65	18 – 52	
	Bearded seal	Protein	$\delta^{13}C$	0 – 9		2 – 32
		Protein	$\delta^{13}C$, $\delta^{15}N$	0 – 11	0 – 2	
		Lipid	$\delta^{13}C$	2 – 38	2 – 30	
	Beluga whale	Protein	$\delta^{13}C$	0 – 10		1 – 22
		Protein	$\delta^{13}C$, $\delta^{15}N$	0 – 13	0 – 3	
		Lipid	$\delta^{13}C$	1 – 24	1 – 19	
	Bowhead whale	Protein	$\delta^{13}C$	1 – 20		2 – 51
		Protein	$\delta^{13}C$, $\delta^{15}N$	2 – 19	0 – 4	
		Lipid	$\delta^{13}C$	2 – 59	2 – 47	
Male	Ringed seal	Protein	$\delta^{13}C$	62 – 86		15 – 44
		Protein	$\delta^{13}C$, $\delta^{15}N$	63 – 78	13 – 16	
		Lipid	$\delta^{13}C$	2 – 35	2 – 28	
	Bearded seal	Protein	$\delta^{13}C$	0 – 13		2 – 41
		Protein	$\delta^{13}C$, $\delta^{15}N$	0 – 14	0 – 3	
		Lipid	$\delta^{13}C$	3 – 47	2 – 38	
	Beluga whale	Protein	$\delta^{13}C$	0 – 15		10 – 33
		Protein	$\delta^{13}C$, $\delta^{15}N$	1 – 17	0 – 3	
		Lipid	$\delta^{13}C$	13 – 38	10 – 30	
	Bowhead whale	Protein	$\delta^{13}C$	2 – 32		3 – 52
		Protein	$\delta^{13}C$, $\delta^{15}N$	7 – 27	1 – 5	
		Lipid	$\delta^{13}C$	3 – 59	2 – 47	

Fig. 3.1 Photographs of various type and size of prey commonly eaten by polar bears in the Beaufort Sea. Prey items are shown in order of size, smallest to largest. a) Newborn ringed seal pup (muscle and small amount of blubber available can be consumed by a polar bear in one meal), b) adult ringed seal (muscle and blubber components can be eaten by a polar bear in one meal), c) adult bearded seal (blubber alone can satiate a polar bear) and d) bowhead whale carcass (blubber alone can satiate several polar bears). A pencil (14cm) in photograph A and saw (47cm) in photographs B and C are shown for size references.

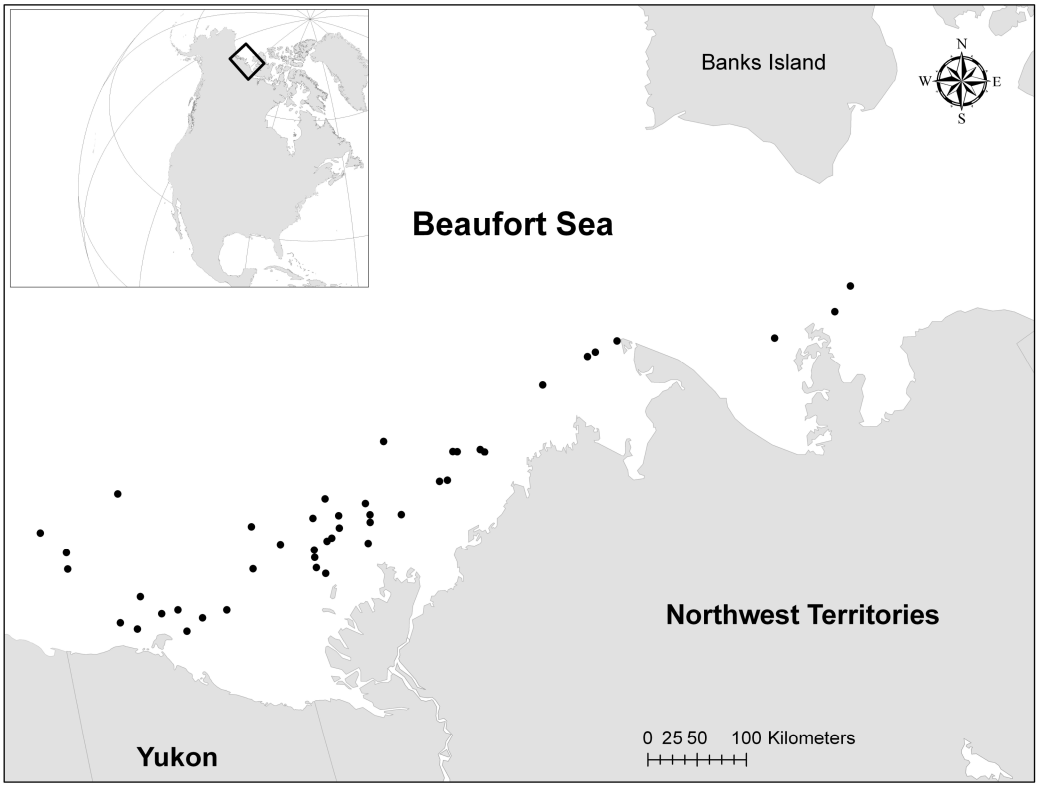

Fig. 3.2 Map of study area showing polar bear capture locations in the Beaufort Sea (2005).

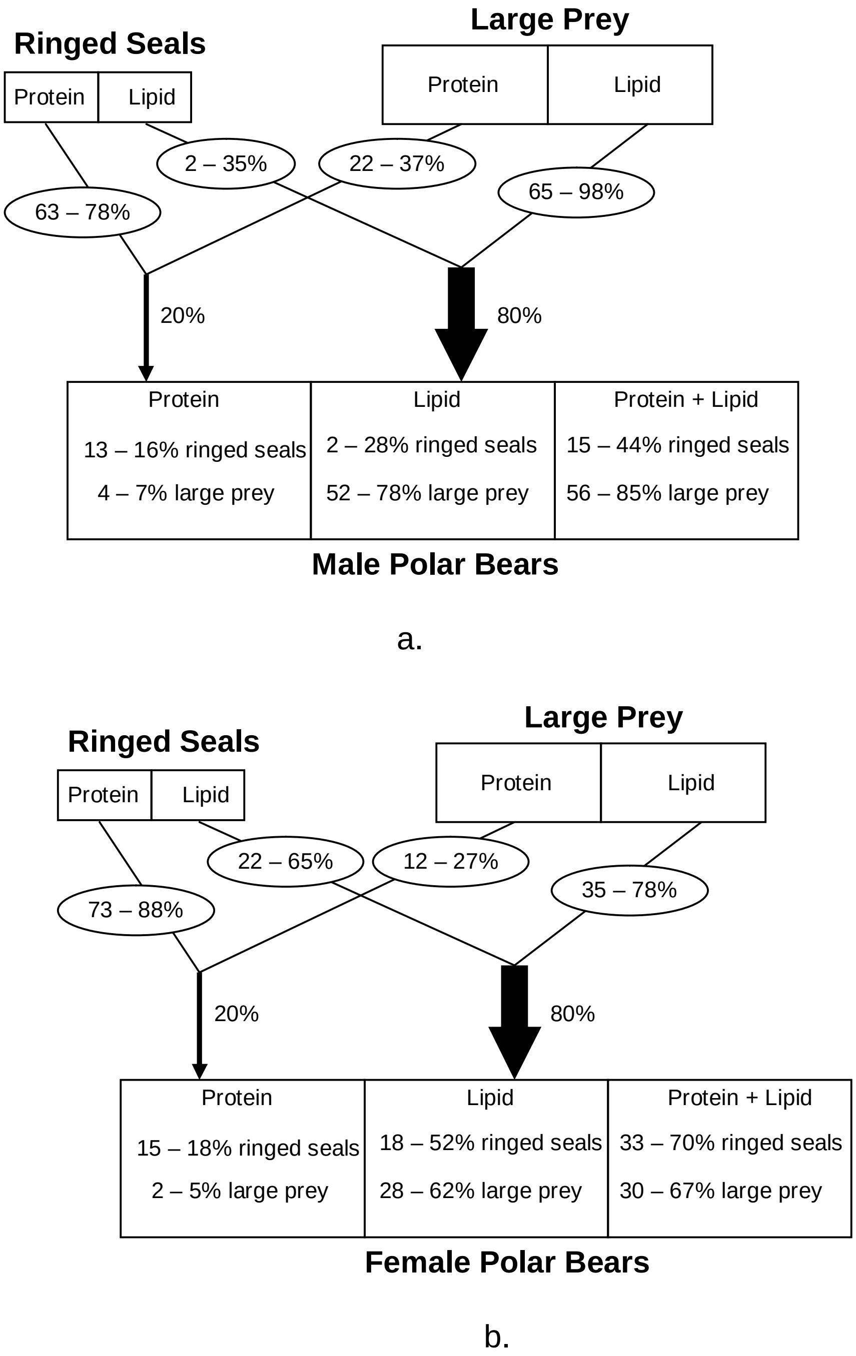

Fig. 3.3 Flow chart diagram showing contributions of protein and lipid from ringed seals and large prey to (a) adult male polar bears and (b) adult female polar bears. Source contributions were estimated separately for protein- and lipid-metabolic pathways and represent 5th to 95th percentiles of MixSIR estimates. All large prey sources were combined *a posteriori* (Phillips et al. 2005). The

contributions to the protein-metabolic pathway were adjusted to amount to 20% of the overall diet, whereas contributions to the lipid-metabolic pathway were adjusted to amount to 80% (based on Best 1985).

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Chapter 4

Polar bear migratory patterns and seasonal fidelity in relation to sea ice dynamics

4.1 Introduction

Migration is a behavioral adaptation to seasonal environmental fluctuations and an integral component of the life history of numerous mobile species (Fryxell and Sinclair 1988, Laidre et al. 2004, Dingle and Drake 2007). The predictable and recurrent nature of many phenological processes allows migratory species to maximize energy gains by altering seasonal habitat use to overlap with abundant or accessible nutritional resources (Tynan and DeMaster 1997, Rojas-Martinez et al. 1999, Alerstam et al. 2003, Rasmussen et al. 2007). In addition, migration is often associated with seasonal fidelity to familiar areas, which can increase foraging efficiency and the likelihood of reproductive success (Greenwood and Harvey 1982, Switzer 1993, Brown et al. 2008, Peron et al. 2010). Increasing global temperatures have altered the timing of numerous phenological events and consequently disrupted the migratory behaviour and seasonal habitat use of several species (Stefanescu et al. 2003, Rosenzweig et al. 2008, Saino et al. 2009, Sharma et al. 2009). Disruptions to migratory patterns, seasonal philopatry, and timing of natural phenological events will likely have negative energetic and reproductive consequences for numerous migratory wildlife populations (Post and Forchhammer 2008, Bronson 2009, Milligan et al. 2009). Quantifying ecological connections between environmental factors and the seasonal distribution of populations is thus of particular importance when examining potential effects of climate-induced environmental changes (Post and Forchhammer 2002).

Polar bears (*Ursus maritimus*) in the Western Hudson Bay subpopulation display annual migration patterns on- and off-land that are closely linked to sea ice phenology. In early to mid summer, when sea ice in Hudson Bay completely melts, polar bears migrate to on-land refugia and spend ice-free months relying on endogenous fat reserves during an extended fast (Lunn and Stirling 1985, Ramsay and Stirling 1988, Stirling and Derocher 1993). Pagophilic seals, the primary prey of polar bears, are inaccessible without a sea ice platform from which to hunt (Stirling and Derocher 1993, Ferguson et al. 2000, Derocher et al. 2004). When sea ice melts to the stage that highly fractured ice makes mobility inefficient, polar bears are forced to head for land. Although some terrestrial foraging by polar bears has been reported (Derocher et al. 1993, Stempniewicz 2006), terrestrial foods do not contribute substantially to their annual energy budget (Ramsay and Hobson 1991, Hobson et al. 2009). Therefore, yearly migration between marine and terrestrial environments represents movement between habitat with a positive energy state and habitat with a negative energy state. The annual return to sea ice when it re-freezes in the fall represents a switch-over back to a state where polar bears can again gain energy from marine resources.

Increasing evidence suggests that rising global temperatures are altering the timing and magnitude of seasonal sea ice distributions and disrupting annual movement patterns of many Arctic marine mammals (Tynan and DeMaster 1997, Freitas et al. 2008, Moore 2008), including polar bears (Stirling et al. 1999, Stirling and Parkinson 2006, Gleason and Rode 2009). Understanding the relationship between seasonal sea ice distribution and Western Hudson Bay polar bear movement patterns is essential when examining potential effects of climate-induced environmental changes because earlier break-up reduces the on-ice feeding period and extends the on-land fasting period. Empirical studies indicate that earlier break-up has been linked to declines in polar bear body condition, reproduction, and population numbers (Stirling et al. 1999, Regehr et al. 2007). Additionally, modeling has suggested that delayed freeze-up in Hudson Bay could further lengthen the annual fasting period and reduce survival rates (Molnar et al. 2010). Climate-induced lengthening of the summer fasting period exemplifies how phenological events related to a species life history can be disrupted by rising global temperatures. Similar instances have been observed in other wildlife taxa throughout the world (Walther et al. 2002).

In addition to altering the timing of migration, changes to sea ice freeze-thaw cycles affect the seasonal geographic distribution of polar bears (Mauritzen et al. 2003, Schliebe et al. 2008, Durner et al. 2009). Seasonal site fidelity has been deemed beneficial for many animals due to the energetic efficiency associated with accessing familiar resources such as food or quality breeding sites (Baker et al. 1995, Deutsch et al. 2003, Mansfield et al. 2009). Polar bears show a high degree of fidelity to terrestrial refugia along the Manitoba coast between the Churchill and Nelson Rivers (Fig. 4.1) (Derocher and Stirling 1990, Lunn et al. 2004, Stirling et al. 2004). Mark and recapture studies on polar bears in western Hudson Bay indicate adult females have mean distances of 33 km between annual on-land recapture locations (Derocher and Stirling 1990). Fidelity to specific onshore regions likely reduces the energetic demands of searching for suitable summer habitat. The Western Hudson Bay polar bear denning area has been used for several hundred years by pregnant females that display a high degree of fidelity to these specific areas (Ramsay and Stirling 1990, Scott and Stirling 2002). Females travel to the same denning area every year, which may allow them to show offspring where appropriate denning habitat occurs (Derocher and Stirling 1990, Stirling et al. 2004). Counterclockwise currents along the western coast of Hudson Bay carry the last remaining ice during break-up to regions adjacent to Manitoba and Ontario (Wang et al. 1994, Gough and Allakhverdova 1999, Saucier et al. 2004) and these ice movement patterns likely influence observed fidelity to this area. How changes to the timing of sea ice break-up will affect fidelity of polar bears to onshore denning areas is unknown. Earlier break-up may result in bears either leaving the sea ice early and continuing to show site fidelity or extending their on-ice period by remaining on the ice that drifts further south towards the Ontario coast. Both options have potential costs because leaving the ice early results in reduced food intake and an extended fast, while drifting southward forces bears to travel back on land or use unfamiliar territory in southern Hudson Bay during the ice-free period. Southern portions of Hudson Bay are the last regions to re-freeze in the fall (Gough and Allakhverdova 1999) and spending the ice-free period in these areas would result in a longer onshore fast.

Using satellite-linked telemetry, I examined how the timing of specific ice concentrations during break-up and freeze-up and the rates of ice disappearance and formation affect migration patterns of polar bears. I also examined temporal trends in the dates polar bears from the Western Hudson Bay subpopulation migrate on and off land. Trends towards earlier break-up (Gagnon and Gough 2005a, Stirling and Parkinson 2006, Scott and Marshall 2010) and later freeze-up (Gagnon and Gough 2005a, Towns et al. 2009, Hochheim and Barber 2010) have been documented within Hudson Bay. I hypothesized these trends in the timing of break-up and freeze-up would correspond with trends in the timing of polar bear migrations between terrestrial and marine habitats. Finally, I analyzed movement data from collared polar bears to determine if the timing and rate of sea ice break-up as well as geographic distribution of sea ice affect fidelity to on-land regions.

4.2 Materials and Methods

Polar bears were captured along the western coast of Hudson Bay between Churchill, Manitoba and the Ontario border (Fig. 4.1). Bears were located from a helicopter and immobilized via remote injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratories Virbac, Carros, France; Stirling et al. 1989). All captures occurred on land either in August/September (autumn) when bears were ashore during the ice-free season or in February/March (spring) when females were emerging from maternity dens with cubs-of-the-year. In

1991-97, 46 Doppler shift Argos® satellite-linked collars (Telonics, Mesa, Arizona) were deployed on 41 different adult female polar bears with collars replaced on 5 bears. The frequency of locations obtained by Doppler shift collars varied depending on short-term research objectives and transmission intervals ranged from 2 to 10 days. In 2004-09, 74 global positioning system (GPS) Argos® satellite-linked collars (Gen III and IV collars, Telonics, Mesa, AZ) were deployed on 68 adult females. These collars were programmed to obtain one GPS location every four hours. No collars were deployed between 1998 and 2004. Collars were put on adult females with either cubs-of-the-year or one-year-old cubs.

Data from the newer GPS collars were subsampled to match the mean location interval of Doppler shift collars. Because Doppler shift collars had location frequencies of up to several days, dates ashore and departure from shore dates tended to be overestimated relative to GPS collars that detected these events within hours of when they actually occurred. After subsampling, all location intervals were consistent at the lowest temporal resolution allowing for relative long-term trend analysis in estimated dates polar bears migrated on and off land and correlations with associated environmental conditions. A geographic information system (ArcInfo 9.3, Environmental Systems Research Institute, Redlands, California) was used to extract daily ice concentrations approximated from daily Special Sensor Microwave/Imager (SSM/I) passive microwave data obtained from the National Snow and Ice Data Center (Boulder, Colorado). Sea ice concentrations were analyzed at a resolution of 25 x 25 km cells. Daily sea ice concentrations were determined using the mean concentration value from all pixels within analysis-specific regions of interest.

I examined a number of linear regression models to assess the timing of specifc sea ice concentrations and the rate of ice disappearance as predictor variables potentially correlated to dates polar bears arrived ashore (Table 4.1). I defined date ashore for collared bears as their first location on land that was not followed by a location off-shore until the following autumn freeze-up. Linear regression models were built to determine if dates polar bears arrived ashore were related to the date that any of several sea ice concentration values occurred, starting at 90% and decreasing in 10% increments. The timing of these *a priori* increments represented an evenly distributed range of sea ice conditions from the beginning to end of annual break-up. Ice concentrations for these analyses were derived from an area within a 95% minimum convex polygon (MCP) determined from on-ice polar bear locations collected throughout the entire study (Fig. 4.1). The date of each 10% sea ice concentration increment was determined using the first day mean ice concentration became ≤ the given increment value. Linear regression models also included a variable to test whether the number of days it took ice to disappear from the given concentrations affected dates ashore. The date sea ice concentration became ≤ 5% was considered ice disappearance. Thus, a set of linear regression models was tested for each sea ice concentration increment with combinations of the above two predictor variables and their interaction terms (Table 4.1).

Similar sets of regression models were used to determine which sea ice predictor variables best corresponded to dates polar bears departed from shore during freeze-up (Table 4.2). Departure from shore date was defined as the first location off-shore that was not followed by a location on land until break-up the next year. Sets of linear regression models were built for dates during freeze-up when each of several sea ice concentration values occurred in the 95% MCP, starting at 10% and increasing in 10% increments. The date of each 10% sea ice increment was determined using the day sea ice concentration became ≥ the given increment value. These linear regression models also used a variable to test whether the number of days it took for ice to freeze to the given concentration increment starting from the date sea ice concentration became ≥ 5% affected departure from shore dates. Each set of models used combinations of the above two predictor variables and their interaction terms (Table 4.2). Departure from shore dates during freeze-up are lacking for 1993 because collars were not deployed that year. I also examined temporal relationships in polar bear migration patterns. A linear regression model was used to analyze the relationship between year and ashore dates and a separate linear regression was used to examine the relationship between year and departure from shore dates.

Finally, I tested various sea ice predictor variables hypothesized to affect the fidelity of polar bears to the western Hudson Bay coast. I used the distance between a bear’s capture location and where they came ashore during break-up the following year as a measurement of fidelity. Predictor variables in the best fitting model describing dates polar bears arrived ashore were considered in potential linear regressions to test whether changes to the timing of these events affected fidelity. In addition, I hypothesized the relative distribution of sea ice during break-up may differ among years and consequently affect where polar bears arrive on land. To examine the distribution of sea ice as it pertains to where polar bears may come to shore during break-up, I compared daily ice concentrations for two regional zones along the coast of western and southern Hudson Bay (Fig. 4.1). These two regional coastal zones were chosen because they encompassed all locations where collared bears came ashore, except for one that came ashore on Long Island in SE Hudson Bay. Each regional coastal zone extended 150 – 200 km off-shore because bears travel through these coastal areas immediately prior to arriving on land and it is also where the last ice typically remains before final break-up (Stirling et al. 2004). These two regions also represented areas known to differ significantly from one another in the timing of break-up (Stirling et al. 2004). In addition, the line dividing regional coastal zones runs along the boundary between Western and Southern Hudson Bay subpopulations (Aars et al. 2006). Most collared bears came ashore in the coastal zone within the Western Hudson Bay subpopulation; however, some collared bears came to shore further south within the Southern Hudson Bay subpopulation. The relative amount of ice in the southern zone compared to the western zone was used as a metric to describe sea ice distribution during break-up. This predictor variable was determined by dividing the ice concentration in the southern zone by that in the western zone on the date of the given sea ice concentration increment that best corresponded to date ashore (as determined by previously described regression models). In years that GPS collars were used, locations that bears came ashore were determined using the first location on land determined by the highest temporal resolution data available (i.e. not data subsampled to match the Doppler shift collar location frequencies). Linear regression models were used to examine fidelity in relation to all combinations of potential predictor variables and two-way interactions. All fidelity regression models used heteroskedasticity-robust standard errors.

Akaike's Information Criterion (AIC) was used to separately test the relative support for various models examining predictor variables related to dates ashore, departure from shore dates, and fidelity (Burnham and Anderson 2002). Models within two AIC units of the best model were considered to have similar support unless they had a higher number of parameters than the best model (Arnold 2010). Statistical analyses were done in STATA 10 (Stata Corporation, College Station, Texas, USA). Unstandardized beta parameter estimates (β) and 95% confidence intervals are provided for each predictor variable. Variance inflation factors for all variables included in regression models were < 10, indicating multicollinearity was not a concern (Allison 1999).

4.3 Results

I recorded 76 dates ashore in 1991-1999 and 2005-2009 and 105 departure from shore dates in 1991-1992, 1994-1997, and 2004-2009. Collar malfunctions and/or dropped collars affected sample size. Mean annual sample sizes were 5.4

(S.E. = 0.9) for dates ashore and 8.8 (S.E. = 1.3) for departure from shore dates. The best fit regression model for predicting polar bear dates ashore used the date of 30% sea ice concentration during break-up, the number of days between 30% sea ice concentration and ice disappearance, and the interaction between these two variables (Model $F_{3, 72} = 10.71$, $P < 0.001$). Examination of the parameter estimates for the best model indicated that all parameters included were strong predictors for date ashore (Table 4.3). Relatively earlier dates of 30% ice concentration, faster disappearance of sea ice during break-up, and the combined effects of these variables resulted in earlier dates ashore for collared bears. Throughout the study, bears arrived ashore a mean of 28.3 days (S.E. = 7.8) after 30% ice-cover (Fig. 4.2).

The best fitting regression model predicting when polar bears departed from shore used the date of 10% sea ice concentration during freeze-up and the number of days between appearance of ice and 10% ice concentrations (Model $F_{3, 102} = 29.02$, $P < 0.001$). Examination of the parameter estimates for the best model indicated that all parameters included were strong predictors for departure from shore dates (Table 4.4). Relatively later dates of 10% sea ice concentration and slower ice formation during freeze-up tended to result in delayed departure from shore dates. Collared polar bears left shore an average of 2.3 days, S.E. = 0.69, after 10% freeze-up (Fig. 4.2).

Dates ashore for collared bears showed a temporal trend towards occurring earlier ($\beta = -0.88$, CI = -1.51 to -0.26, $P < 0.01$) and departure from shore dates showed a trend towards occurring later ($\beta = 0.66$, CI = 0.42 to 0.90, $P < 0.001$).

The distances between polar bear capture locations and where they came to shore during break-up in subsequent year(s) ranged from 3 to 720 km (mean = 118, S.E. = 17). Throughout the study 12% of the arrival ashore locations occurred outside the western zone. If bears did not arrive ashore within the western zone, they typically came to shore further south and east. Only one bear came ashore north of Churchill (approximately 20 km north of the municipality in 2008). The lowest degree of fidelity occurred in 2007, when 4 of 9 females came to shore in the southern zone. Additionally, in 2007, 3 bears came to shore between the Ontario border and Nelson River (Fig. 4.1).

The best fit model for predicting fidelity of polar bears included: number of days between date of 30% ice concentration during break-up and ice disappearance, ice concentration in the southern Hudson Bay zone relative to the western Hudson Bay zone, and the interaction between these two variables. Examination of the parameter estimates for this model indicated the number of days between 30% ice concentration during break-up and ice disappearance was a weak predictor of fidelity, but ice concentration in the southern Hudson Bay zone relative to the western Hudson Bay and the two-way interaction term were strong predictors of fidelity (Table 4.5). Polar bears tended to show less fidelity when there was relatively more ice present in the southern Hudson Bay zone compared to the western Hudson Bay zone, and this pattern was exacerbated when rates of ice disappearance were relatively high (Table 4.5).

4.4 Discussion

Highly mobile marine predators have few barriers to impede their movement so factors determining their geographic distribution and migration patterns are likely linked to fluctuations in environmental conditions, the spatiotemporal distribution of resources, and energetic benefits received from site fidelity (Vibe 1967, Cotté et al. 2009, Jorgensen et al. 2009). In this study I examined how the dynamic nature of an Arctic sea ice ecosystem, with strong intra- and inter-annual variations in ice distribution, can affect the migration patterns and seasonal fidelity of an upper level marine predator, the polar bear. Polar bear migratory behaviour between land and sea ice environments was linked to specific sea ice conditions that occurred during annual break-up and freeze-up periods. Previously, annual mean arrival ashore dates for polar bears in western Hudson Bay were correlated with the timing of 50% ice concentration during break-up (Stirling et al. 1999). Using higher resolution daily sea ice data, and testing a range of ice concentration increments, I found that polar bear dates ashore were more closely correlated with the timing of 30% sea ice concentration during break-up. I additionally determined that timing of 10% ice concentration during freeze-up was correlated with polar bear departure from shore dates (Fig. 4.2). Such knowledge regarding how large-scale environmental factors are correlated to the timing of migration is imperative to conservation efforts for migratory species (Mueller et al. 2008, Harris et al. 2009, Jonker et al. 2010); particularly those inhabiting geographic regions greatly affected by climate change (Laidre et al. 2008). Climate change scenarios for Arctic and sub-Arctic environments forecast long-term increases in atmospheric temperatures coupled with changes to sea ice freeze-thaw cycles (Gagnon and Gough 2005b, Holland et al. 2006, Zhang and Walsh 2006). Therefore, the close relationships identified between regional ice phenological events and polar bear migration patterns are especially relevant to understanding the effects of increased atmospheric temperatures on polar bears. Monitoring of the timing of ice concentrations correlated with polar bear migration will provide valuable insight regarding changes to the length of onshore fasting periods for polar bears in western Hudson Bay.

In addition to the timing of specific sea ice concentrations during break-up and freeze-up, the rates of ice disappearance and ice formation were also correlated with polar bear migration patterns. When ice disappeared at higher than normal rates during break-up, polar bears were likely forced to move more quickly towards shore. Conversely, when ice formation was relatively slower during freeze-up, polar bears may have had a delayed response to the appearance of ice causing a lag in the timing of departure from shore dates. Timing and rate of ice disappearance and formation are dependent upon numerous interacting factors related to trends in atmospheric circulation, wind direction, and atmospheric temperatures (Mysak et al. 1996, Wang et al. 2004, Hochheim and Barber 2010). My results suggest that knowledge regarding how these factors are affected by anthropogenic greenhouse gases will be a crucial component of predicting future polar bear migration behaviour in relation to climate change. In addition to climate-induced shifts to annual patterns of sea ice cover, decreased ice thickness throughout Arctic regions is also likely to affect ice-dependent marine ecosystems (Moline et al. 2008). Decreases to ice thickness will probably further hinder polar bear mobility through highly fractured ice during break-up, which may force bears to abandon the sea ice and head for land at an earlier date.

The specific ice concentration that predicted polar bear departure from shore dates during freeze-up was lower than that which predicted dates ashore during break-up. In Hudson Bay, freeze-up typically occurs in the western portion first, with ice forming along the north-west shoreline and spreading south-east (Derocher and Stirling 1990, Gough et al. 2004). When total ice cover in the 95% MCP was 10%, most of the existing ice was distributed along the western coast where polar bears aggregate to await freeze-up (Latour 1981, Derocher and Stirling 1990). Thus, the local ice concentrations that bears were exposed to when departing from shore were actually greater than 10%. During break-up polar bears and ice are usually dispersed more broadly throughout Hudson Bay (Stirling et al. 2004) and therefore total ice concentration values predicting migration onto shore are not comparable to those which predict migration back onto the sea ice during freeze-up. Even though ice distribution differs significantly during late stages of break-up versus early stages of freeze-up, quantifying total concentrations in the western Hudson Bay region is a useful technique to predict seasonal movements and effects of changing environmental conditions at the population level. For many species that undergo annual migrations, environmental cues that correspond to migratory patterns may be seasonally dependent and thus differ with the direction of movement and anticipated destination (O'Reilly and Wingfield 1995, Ramenofsky and Wingfield 2007). Therefore, environmental signals correlated with the occurrence of spring directional movements often differ from those most commonly associated with autumn movement patterns. Changes to the timing of migration patterns as a result of varying environmental conditions have been observed in several species (Sims et al. 2004, Swanson and Palmer 2009, Srygley et al. 2010) and may lead to disruptions in the spatiotemporal overlap with key resources (Robinson et al. 2008). Throughout my study, collared polar bears showed trends towards arriving onshore earlier during break-up and departing from shore later during freeze-up. The consequent reductions to the amount of time polar bears had access to pagophilic seal prey likely resulted in negative effects to reproduction and survival (Derocher and Stirling 1995, Stirling et al. 1999, Regehr et al. 2007, Molnar et al. 2010). Additionally, nutritional stress associated with later departure from shore dates during freeze-up has been linked to increases in human-bear conflicts in the western Hudson Bay region (Towns et al. 2009).

Climate-induced environmental changes that alter the timing of ecologically relevant phenological events have the potential to negatively impact specialist species with high degrees of seasonal fidelity; however, responses and adaptations to these changes are likely to vary. For example, animals that demonstrate particularly strong site fidelity may not alter their distribution despite decreases to habitat quality (Ganter and Cooke 1998, Laidre and Heide-Jørgensen 2005, Matthews and Haiganoush 2010). Conversely, some animals may shift their distribution but as a consequence be constrained to unfamiliar or poorer quality habitat (Ficke et al. 2007, Stillman and Goss-Custard 2010). Because ice usually remains later in southern Hudson Bay (Wang et al. 1994, Gough and Allakhverdova 1999, Saucier et al. 2004), I hypothesized polar bears from western Hudson Bay may come to shore further south and east along the Ontario coast in years with early break-up. In 2007, a high proportion of collared polar bears came to shore in Ontario or south-east of the area where they were previously captured during the summer. However, I found that polar bears displayed high degrees of fidelity even when sea ice disappeared relatively earlier than normal, suggesting that coming ashore in a familiar location is more important than remaining longer on the ice (Derocher and Stirling 1990, Stirling et al. 2004). For many wildlife species, the choice to abandon site fidelity represents a balance between risks associated with using unfamiliar habitat and benefits associated with potentially maximizing energy acquisition by moving to new areas (Greenwood 1980, Bensch and Hasselquist 1991, Bradshaw et al. 2004). For female polar bears, additional energy gained from extra hunting on the last sea ice that drifts south may not outweigh risks to reproductive success caused by spending shore-bound or maternity denning periods in unfamiliar areas. Similarly, energetic benefits gained from extended hunting in southerly locations may not outweigh the costs associated with walking on land back to familiar habitat.

Observed lower fidelity in certain years was due to numerous environmental conditions affecting the distribution of sea ice during break-up, which likely negatively affected the ability of some bears to arrive on land in the vicinity of their preferred summer habitat. Variable winds and localized atmospheric and oceanic temperature anomalies (Etkin 1991, Barry et al. 1993, Comiso 2006) may have caused annual differences in the relative ice concentrations between southern and western zones during break-up, which affected fidelity to a larger degree when rate of ice disappearance was high. Climate change has been predicted to increase future high wind events and positive local temperature anomalies during breakup in Hudson Bay (Knippertz et al. 2000, Joly et al. 2010), which is likely to affect both the distribution of sea ice and rate of ice disappearance. Therefore, under current climate change scenarios, I expect to observe future decreases in polar bear fidelity to specific onshore regions.

Successful wildlife management relies upon knowledge of population or subpopulation boundaries that exist because a group of animals show annual or seasonal fidelity to specific regions (Kufeld et al.1989, Bethke et al. 1996, Van Dyke et al. 1998). However, changing environmental conditions can alter fidelity and obscure population boundaries. For instance, populations of mule deer have been shown to vary their winter range depending on atmospheric temperatures, which can complicate censusing efforts (Brown 1992). However, when the effects of varying environmental conditions on fidelity are known, appropriate measures may be taken to compensate for shifting population ranges. If future conditions cause decreased seasonal fidelity for western Hudson Bay polar bears, managers are likely to face increasingly frequent challenges associated with obscured population boundaries during the summer onshore period. Similarly, Derocher et al. (2004) predict polar bear population boundaries are likely to be altered throughout the Arctic because of climate induced changes to sea ice distribution and habitat connectivity.

The strong link between phenological events and seasonal distributions of migratory wildlife populations highlights the importance of quantifying relationships between environmental cues and animal movements. Understanding how large-scale seasonal environmental conditions affect the timing of synchronized movement patterns is crucial for the successful implementation of conservation and management measures to sustain wide-ranging species that display high degrees of seasonal fidelity. Polar bears were once believed to be circumpolar nomads; however, observations of philopatric tendencies have resulted in the recognition of discrete subpopulations distributed throughout the Arctic (Paetkau et al. 1995). The relative cohesiveness of these subpopulations is an important aspect of current polar bear population monitoring and management (Aars et al. 2006). My results indicate that under certain environmental conditions, decreases in polar bear fidelity to summer onshore refugia can occur. Climate change is predicted to alter weather patterns and environmental conditions, not only in Arctic ecosystems, but globally (ACIA 2005). These climate-induced environmental changes will likely alter the distribution and geographic population structure for numerous plant and wildlife species and result in new challenges for scientists and mangers seeking to quantify and monitor population dynamics and community composition.

Table 4.1 Example of candidate linear regression models to predict polar bear date ashore for one of several a priori sea ice concentrations (i.e. 90%) occurring during spring break-up within the 95% MCP. Identical models were tested for all sea ice concentration increments between 90 – 10% at 10% increments. *Definitions of variables*: 90% sea ice is the date of 90% sea ice concentration during break-up, 90% to disappearance is the number of days between date of 90% sea ice concentration and ice disappearance.

Model number	**Model**
1	90% sea ice
2	90% to disappearance
3	90% sea ice, 90% to disappearance
4	90% sea ice, 90% to disappearance, 90% sea ice*90% to disappearance
37	Null

Table 4.2 Example of candidate linear regression models to predict polar bear departure from shore dates for one of several a priori sea ice concentrations (i.e. 10%) occurring during autumn freeze-up within the 95% MCP. Identical models were tested for all sea ice concentration increments between 10 – 90% at 10% increments. *Definitions of variables*: 10% sea ice is the date of 10% ice concentration during freeze-up, appearance to 10% is the number of days between the first appearance of sea ice and date of 10% sea ice concentration.

Model number	**Model**
1	10% sea ice
2	appearance to 10%
3	10% sea ice, appearance to 10%
4	10% sea ice, appearance to 10%, 10% sea ice*appearance to 10%
37	Null

Table 4.3 Parameter estimates, SE, and 95% confidence intervals (CI) for parameters in the best model for polar bear date ashore.

Parameter	Estimate	SE	95% CI		P-value
			Lower	Upper	
30% sea ice	3.36	1.06	1.28	5.44	< 0.01
30% to disappearance	39.16	15.0	9.84	68.48	< 0.01
30% sea ice*30% to disappearance	-0.21	0.08	-0.37	-0.05	0.01
Constant	-403.13	192.37	-780.17	-26.09	< 0.05

Table 4.4 Parameter estimate, SE, and 95% confidence interval (CI) for parameter in the best model for polar bear departure date.

Parameter	Estimate	SE	95% CI		P-value
			Lower	Upper	
10% sea ice	0.74	0.11	0.52	0.96	< 0.001
Appearance to 10%	1.15	0.51	0.14	2.15	< 0.05
Constant	83.63	36.45	12.18	155.08	< 0.05

Table 4.5 Parameter estimates, robust standard errors (SE), and 95% confidence intervals (CI) for parameters in the best models for polar bear fidelity. Polar bear fidelity was defined as the distance between a bear's capture location and where they came ashore during break-up the following year. *Definitions of variables:* 30% to disappearance is number of days between date of 30% ice concentration during break-up and ice disappearance, SH/WH at 30% is ice concentration in the southern Hudson Bay zone relative to the western Hudson Bay zone.

Parameter	Estimate	SE	95% CI		P-value
			Lower	Upper	
30% to disappearance	14.08	8.08	-1.76	29.92	> 0.05
SH/WH at 30%	195.21	65.63	66.57	323.84	< 0.01
30% to disappearance* SH/WH at 30%	-10.66	4.55	-19.57	-1.74	< 0.05
Constant	-177.61	123.83	-420.30	65.09	> 0.05

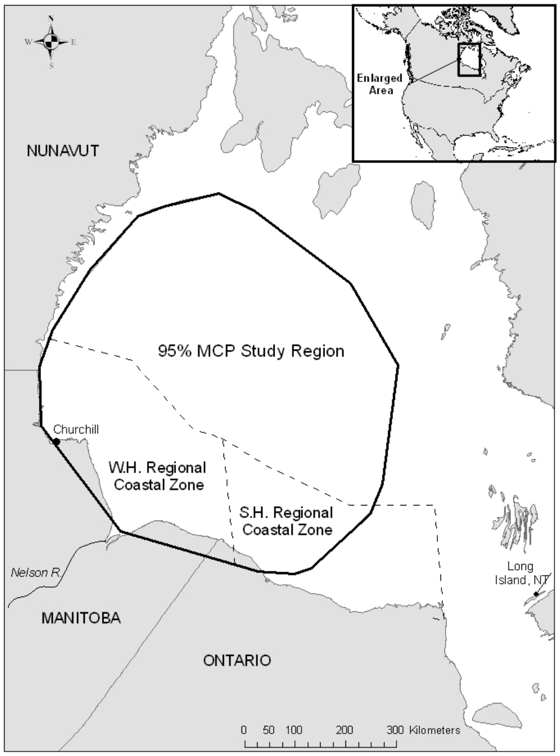

Fig. 4.1 Map of Hudson Bay showing the 95% minimum convex polygon of all marine polar bear locations (1991-97 and 2004-09) and the two regional coastal zones.

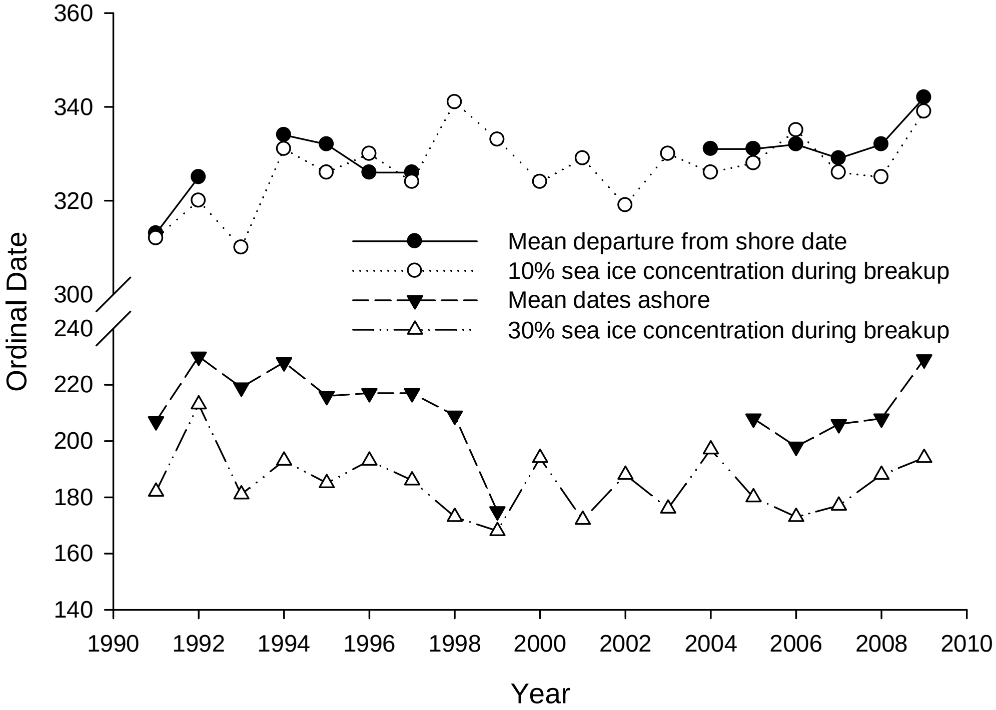

Fig. 4.2 Dates of sea ice concentrations that best corresponded to dates ashore during breakup and departure from shore dates during freeze-up for collared polar bears in western Hudson Bay. Dates ashore and departure from shore dates are shown as annual means for all collared polar bears.

4.5 Literature Cited

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Chapter 5

Habitat-mediated timing of annual migration in polar bears: an individual perspective

5.1 Introduction

Understanding how populations of animals respond to seasonal environmental shifts or long-term habitat change often involves measurements of interacting factors at large geographic scales (Stenseth et al. 2002, Parmesan et al. 2005, Hone and Clutton-Brock 2007). Once acquired, baseline knowledge of landscape-scale ecological relationships is useful for assessing implications of global or regional environmental change on population viability and distribution (Thomas et al. 2004, Austin and Rehfisch 2005, Van de Pol et al. 2010). However, additional appreciation for how local habitat characteristics influence individuals is often required because fine-scale ecological relationships may differ from those measured at landscape scales, especially in heterogeneous habitats (Wiens 1989, Kuefler and Haddad 2006, Murray et al. 2008). Measuring ecological relationships at multiple spatial scales is therefore necessary to gain awareness of the mechanisms behind population responses to environmental change, such as habitat-mediated migration. Migration represents a distinct type of animal movement observed across a vast array of taxa. There are numerous types and degrees of migratory behaviour (Dingle and Drake 2007); however, in its simplest form migration is a round-trip movement between isolated areas at different times of the year (Ball et al. 2001, Berger 2004).

Polar bears (*Ursus maritimus*) are wide-ranging carnivores whose circumpolar distribution is associated with ice-covered seas. In southern portions of their range, such as western Hudson Bay, polar bears exhibit annual migrations to land that coincide with sea ice break-up during the summer thaw (Stirling et al. 1999, Stirling et al. 2004, Chapter 4). In southern regions, polar bear movement from marine to terrestrial environments is a necessary migration caused by complete melting of the sea ice platform. Ultimately, the timing of sea ice melt has been associated with polar bear body condition, survival, and reproduction (Derocher and Stirling 1995, Stirling et al. 1999, Regehr et al. 2007, Molnar et al. 2010). Inter-annual variation in the timing of when polar bears arrive ashore has been predicted by landscape-scale indices of ice break-up (Stirling et al. 1999, Stirling and Parkinson 2006, Chapter 4). However, little is known about individual responses to localized and finer-scale sea ice dynamics during the summer melt. Given the heterogeneity of sea ice habitat, particularly during break-up (Gagnon and Gough 2005a), it is unlikely that ice conditions measured at landscape and regional scales represent what individual bears are exposed to at local scales. Furthermore, observed intra-population variation in the timing of annual arrival ashore dates is indicative of an underlying mechanistic relationship between sea ice melt and polar bear migration at finer spatial scales than have been previously measured (Stirling et al. 1999, Chapter 4). Understanding how local environmental factors affect individual variation in the timing of migration allows assessment of underlying behavioural responses by polar bears to seasonally changing environmental conditions. Quantifying behavioural responses to disappearing ice may prove useful when predicting ranges of ice concentration thresholds for suitable habitat under various climate change scenarios in different Arctic regions (e.g., Durner et al. 2009, Regehr et al. 2010, Hunter et al. 2010).

A convenient means of exploring causes of variation in the timing of ecological events is time-to-event modeling, which is more commonly known for its applications to survival analysis. Time-to-event models have recently been applied in ecological research to quantify sources of variation in kill rates for predator-prey systems (Merrill et al. 2010) and the timing of various migratory events (Bauer et al. 2008, Fieberg and DelGiudice 2008, Fieberg et al. 2008). These techniques analyze the probability of an event occurring in relation to duration of exposure to various levels of potential explanatory factors rather than simply the conditions present when the event occurs (Hosmer and Lemeshow 1999, Therneau and Grambsch 2000, Cleves et al. 2002). Therefore, time-to-event models are useful for examining polar bear migratory behaviour because a bear’s decision to migrate is likely dependent upon both the ice conditions they experience before heading for land and the duration of exposure to these conditions.

In this study, I used time-to-event models to explore how exposure of individual polar bears to varying environmental conditions influences the timing of their decision to migrate from marine to terrestrial habitats. I hypothesized sea ice concentration and sea ice rate of change that individual bears experienced at the local-scale would be driving factors in their decision to migrate for shore. These environmental factors, measured as averages throughout western Hudson Bay, are known to correlate with polar bear migrations to shore during spring break-up (Stirling et al. 1999, Chapter 4). I also tested whether distance-to-shore at a given time or various individual demographic characteristics could further explain variation in the timing of migration among individual bears.

5.2 Materials and Methods

Polar bear captures occurred in autumn 2004 – 2008 along the western coast of Hudson Bay between Churchill and the Nelson River (Fig. 5.1). Polar bears were located by helicopter and remotely immobilized via injection of tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®, Laboratoires Virbac, Carros, France; Stirling et al. 1989). A total of 59 global positioning system (GPS) Argos® satellite-linked collars (Gen III and IV collars, Telonics, Mesa, AZ) were deployed on 56 different adult females with either cubs-of-the-year or one-year-old cubs. I only used data from collars that gave consistent locations throughout the break-up period until polar bears arrived on land. Complete collar malfunction and the failure of some collars to provide continuous data throughout the break-up period resulted in a reduced data set. Collars were programmed to obtain one GPS location every four hours.

A time-to-event model was used to determine how environmental factors and individual demographic characteristics influenced the dates polar bears began a directional migration towards shore. My time of origin (*t* = 0) and onset of risk were defined as May 1 of each year because this is immediately prior to when sea ice generally begins to melt in Hudson Bay (Saucier et al. 2004). Polar bears were considered to have entered a directional migration towards shore when the distance between their position and the location where they eventually arrived on land began to permanently decrease. Potential covariates in my models describing environmental conditions individual bears experienced included sea ice concentration, sea ice concentration rate of change, and distance-to-shore. Potential covariates describing individual demographic characteristics included age and reproductive status (i.e., presence or absence of offspring during the summer break-up).

Polar bear GPS collar locations were imported into a geographic information system (ArcInfo 9.3, Environmental Systems Research Institute, Redlands, California) to extract environmental covariate data. Sea ice concentrations at each bear location were approximated from daily Special Sensor Microwave/Imager (SSM/I) passive microwave data obtained from the National Snow and Ice Data Center (Boulder, Colorado). Sea ice rate of change was determined as the difference in ice concentration values between a bear’s current and previous location. Distance-to-shore was calculated as the straight-line distance between a given location and the nearest point on any section of mainland surrounding Hudson Bay. Distance-to-shore was included in the analysis because the probability of a bear beginning a directional migration towards shore may depend on their distance from land and geographic location within Hudson Bay. My time-to-event model used a daily time scale and subsampled one GPS location from daily subsets of collar locations. Using a single GPS location per day ensured the temporal and spatioal resolution of the collar data matched that of the SSM/I sea ice data. Mean springtime movement rate for adult female polar bears in western Hudson Bay is 31.2 km/day (Parks et al. 2006) and SSM/I data provide approximated daily ice concentrations at a resolution of 25 x 25 km cells.

A vestigial premolar was extracted from each collared bear to determine age (Calvert and Ramsay 1998). I hypothesized that age and thus experience may influence their movements to shore during break-up. Reproductive status was inferred from knowledge of whether an individual had cubs-of-the-year, yearling cubs, or was alone at the time of capture. Polar bears in western Hudson Bay typically have a three year interbirth interval (Derocher and Stirling 1995) and unless a bear was re-sighted at a later date I used this interval to calculate reproductive status. Cubs are born in November – December and offspring typically accompany their mothers until March – May of their second year (Ramsay and Stirling 1988), and thus I assumed females and two-year-old offspring had separated by the time they began directional movement towards shore. I hypothesized presence or absence of offspring may affect timing of migration. Female polar bears with offspring may begin their migration towards shore in response to different local environmental conditions than lone individuals because offspring are likely less efficient at traveling through highly fragmented ice and open water.

To choose the best type of time-to-event model for my data (i.e., non-parametric, semi-parametric, or any of numerous available parametric models), it was necessary to consider the potential shape of my underlying baseline hazard function (Cleves et al. 2002, Merrill et al. 2010). The shape of an underlying baseline hazard function describes the hazard rate of an event occurring throughout time in the absence of measured covariate effects (Kumar and Klefsjo 1994, Cleves et al. 2002). The hazard rate for polar bears migrating towards shore in the absence of sea ice dynamics is most likely constant with time because polar bears in northerly regions, with less drastic seasonal changes to environmental conditions, rarely travel to land (Thiemann et al. 2008). Pregnant females in these northerly regions often come to land to build maternity dens; however, maternity denning does not occur until later in the year (Messier et al. 1992) and after my study period which ended with arrival on shore. Additional evidence of a constant baseline hazard comes from observations in 1992 when sea ice in Hudson Bay melted much later than normal, due to the eruption of Mount Pinatubo in the Philippines, and polar bears responded by substantially delaying their migration to land (Stirling et al. 1999). The observed delay to migration in 1992 supports the idea that hazard rates for polar bears migrating to land are related solely to specific environmental conditions and would otherwise not change with time. Therefore, I chose to use a parametric underlying baseline hazard in the exponential form, which assumes hazard remains constant with time in the absence of covariate effects (Hosmer and Lemeshow 1999, Therneau and Grambsch 2000, Cleves et al. 2002).

Statistical analyses were done in STATA 10 (Stata Corporation, College Station, Texas). I first used Akaike Information Criterion analysis, corrected for small sample size (AICc), to evaluate relative support for exponential models examining effects of environmental covariates. All combinations of main effects involving environmental covariates were tested. I also examined two-way interactions for environmental covariates; however, interactions were only added to models including both corresponding main effects. Once the best fitting model using environmental covariates was identified, I used it in an additional AICc analysis with combinations of proposed individual demographic characteristics to determine if model fit was improved.

I tested environmental covariates for collinearity using a Pearson's correlation and no variables had $r > 0.65$. I also visually inspected plots of martingale residuals for each covariate to assess covariate functional forms and ensure my data met proportional hazard assumptions (Cleves et al. 2002). To test my assumption regarding an exponential baseline hazard, I assessed whether the overall hazard for my 'events' varied solely with covariates rather than time (Cleves et al. 2002). I included time, measured as ordinal date, as a covariate in the global models from each AICc analysis to test whether time significantly explained observed variation in the overall hazard. In addition, I compared 95% confidence intervals of the coefficients in the global parametric models with equivalent semi-parametric Cox proportional hazards models with the assumption that a well-fitting parametric model should approximate the coefficients of a Cox proportional hazards model (Cleves et al. 2002, Merrill et al. 2010). I expressed the best fitting exponential model using proportional hazard metrics. Proportional hazard parameters describe the change in relative likelihood of polar bears beginning a directional migration towards shore, on any given day, per unit change in given environmental characteristics (Hosmer and Lemeshow 1999, Therneau and Grambsch 2000, Cleves et al. 2002).

5.3 Results

I recorded 21 polar bear migrations from the sea ice to land for 20 different polar bears. The mean date bears began to head for shore was July 13 (SE = 2.2 days, range = June 28 - August 7). There was an average of 5.8 (SE = 0.9) days between the date polar bears began a directional migration towards shore and their first recorded location on land. When polar bears began a directional migration towards shore they were a mean distance of 80.4 km (SE = 10.6, range = 4.4 - 178.5 km) from the coastline.

I found similar support (ΔAICc < 2) for the time-to-event model examining environmental covariates that used sea ice concentration by itself and models that combined sea ice concentration with either distance-to-shore or sea ice rate of change (Table 5.1). However, the model using only sea ice concentration was chosen as the best fitting model because it had one less parameter than the other competing models with ΔAICc < 2 (Arnold 2010).

Addition of various combinations of individual demographic characteristics to the model using the sea ice covariate alone did not improve model fit (Table 5.2). Proportional hazard parameterization of the best model indicated the likelihood of bears heading for shore at a given time increased by a factor of 1.07 per percentage decrease in the daily sea ice concentration (HR = 0.93, SE = 0.02, $P < 0.001$, 95% CI = 0.90 – 0.96).

Examination of the martingale residuals indicated that all covariates were log-linearly related to the hazard and thus did not require transformations. Time was not significant when it was included in the environmental covariate global model ($HR_{time} = 1.04$, S.E. = 0.03, $P = 0.09$, 95% CI = 0.99 – 1.10) or the global model assessing effects of individual demographic characteristics ($HR_{time} = 1.05 \pm 0.023$, $P = 0.07$), which supports my assumption of an underlying exponential baseline hazard. In addition, the coefficients from global exponential models had overlapping 95% confidence intervals with those of equivalent semi-parametric Cox proportional hazards models, indicating that I attained well-fitting parametric models.

To further examine how sea ice affects timing of polar bear migration towards shore, I estimated the instantaneous hazard function or daily rate of failure for various sea ice increments that adequately demonstrated the relationship between changing environmental conditions and daily rates of failure. It was possible to graph the daily rate of failure for various increments of covariate values independent of time because hazard functions in exponential time-to-event models ‘lack memory’ and thus remain constant throughout time at a given covariate value (Cleves et al. 2002). The predicted instantaneous hazard rate or daily rate of ‘failure’ was negligible when polar bears were exposed to daily ice concentrations > 60%; however, it increased as daily ice concentration decreased below 60% (Fig. 5.2). I also estimated failure (one minus ‘survival’) curves from my fitted model, which indicated the change in probabilities throughout time of polar bears exhibiting directional migration towards shore when exposed to given ice concentrations. The predicted probability of a polar bear heading for shore when exposed to various sea ice concentrations throughout time was highest for low daily ice concentrations and negligible for high daily ice concentrations (> 60%) (Fig. 5.3).

5.4 Discussion

There are numerous examples of animal migration events occurring between distinct habitats in conjunction with cyclical environmental change (Pilliod et al. 2002, Brönmark et al. 2008, Ball et al. 2001, Bestley et al. 2010). Understanding migratory behaviour provides insights on fundamental components of the ecology and life history of both individuals and populations (Hobson 1999). In this study, I examined factors affecting the movement of polar bears from marine to terrestrial habitats at the local scale. In particular, I determined what affects intra-population variation in the timing of movement from sea ice to land using time-to-event modeling. I was able to use information regarding the life history of polar bears and their association with ice throughout their circumpolar distribution to predict and test a specific form for my baseline hazard, allowing for the use of parametric time-to-event models. Parametric time-to-event models are advantageous because they can be utilized to estimate expected probability of an outcome or event when particular covariate values are known and specified (Harman et al. 1996).

I found the sea ice concentrations that individual bears experienced were the main determining factors affecting the timing of migration from sea ice to land. My results corroborate, to some degree, recent research that assumes landscape-scale thresholds of > 50% sea ice concentrations are necessary for suitable polar bear habitat (i.e., Schliebe et al. 2008, Durner et al. 2009, Gleason and Rode 2009, Hunter et al. 2010, Regehr et al. 2010). In part, the reasoning behind using > 50% ice concentration as a threshold stems from documented correlations between 50% break-up in western Hudson Bay and mean dates that polar bears arrive ashore for the annual ice-free period (Stirling et al. 1999). More recently, using higher spatial and temporal resolution SSM/I sea ice data, annual dates Western Hudson Bay polar bears arrived ashore correlated with a mean ice concentration metric of 30% and the rate of sea ice melt (Chapter 4). However, actual mean dates polar bears arrived ashore tended to occur approximately 25 – 28 days following both of these landscape-scale metrics of sea ice break-up (Stirling et al. 1999, Chapter 4). Given that sea ice melts throughout the break-up period, as temperatures get progressively warmer, ice concentrations are below these landscape-scale break-up metrics by the time polar bears abandon marine habitat and head for land. In this study I was able to explicitly quantify the relationship between decreasing local ice concentrations during break-up and the probability through time of bears abandoning the marine habitat and taking a directional path towards shore. Because animals are capable of accumulating and using knowledge about the landscapes they move through (Smouse et al. 2010), understanding the causes of cumulative movement patterns requires quantifying relationships between the length of exposure to given environmental conditions and behavioural responses.

My results indicate that extended periods of exposure to what would be considered suboptimal ice concentrations were required before the probability of directional movement towards shore increased substantially. Depending on the region, polar bears typically select for habitat with ice concentrations between 60 - 95% (Ferguson et al. 2001, Mauritzen et al. 2003, Durner et al. 2004, 2009), but have shown selection for ice concentrations as low as 10 – 60% in some areas and at certain times of the year (Arthur et al. 1996, Mauritzen et al. 2003, Durner et al. 2006). During break-up in western Hudson Bay, it may be energetically beneficial for polar bears to stay on the sea ice as it continues to melt below optimal ice concentrations because they can continue to hunt seals knowing they have a relatively short swim to land (Durner et al. 2009). Polar bears are excellent swimmers and have been observed swimming up to 160 km from shore (Øritsland 1969), which is two-times as far as the mean distance Western Hudson Bay bears were when they began their directional path towards land. However, observations of bears drowning in storm events while attempting to cross large expanses of open water exemplify the risk associated with swimming long distances (Monnett and Gleason 2006.) Therefore, the decision for bears in the Western Hudson Bay subpopulation to abandon sea ice probably balances the benefits of increased time hunting for seals and the costs associated with how far they must travel through heavily broken ice or open water to reach land. Polar bears in other regions of the Arctic, especially open ocean areas, are likely less willing to utilize habitat with such low ice concentrations because of the need to avoid becoming stranded in open water far from land or multiyear pack ice. For example, in the Beaufort Sea, polar bears migrate north to multiyear ice refugia over the Arctic Basin when summer-time temperatures cause sea ice to melt over the continental shelf (Durner et al. 2009, Regehr et al. 2010). In these instances, the risks of polar bears getting stranded in open water before making it to multiyear pack ice refugia are high because they are traveling longer distances towards dynamic and receding targets. In contrast, polar bears in western Hudson Bay move relatively shorter distances to a predictable location (i.e., land).

My measurements of daily distance to shore did not affect the probability of polar bears beginning a directional move towards land. Sea ice in Hudson Bay mostly occurs along the western and southwestern coasts during later stages of break-up (Wang et al. 1994, Gough and Allakhverdova 1999, Saucier et al. 2004) and Western Hudson Bay polar bears show high degrees of seasonal fidelity to specific Manitoba coastal regions during the summer ice-free period (Derocher and Stirling 1990, Lunn et al. 2004, Stirling et al. 2004, Chapter 4). Thus, polar bears likely have a propensity during break-up to utilize sea ice habitat in proximity to these coastal regions to avoid having to come ashore in unfamiliar areas (Chapter 4). In this study, my measurement for distance to shore probably did not affect variation in the timing of my events because most bears tended to be relatively close to land and within swimming distance when they began a directional move towards shore.

Sea ice rate of change was another environmental factor that did not affect when individual polar bears began directional movements towards land. At a local scale, it appears as though polar bears respond more to the quantity of ice habitat available and exposure to suboptimal conditions rather than the day-to-day rate at which ice conditions fluctuate. In contrast, metrics for rate of ice change, measured as the number of days for ice to disappear during break-up in western Hudson Bay, influenced inter-annual variation in polar bear migration dates at the population level (Chapter 4). These observations demonstrate how spatial and time scales at which environmental factors are measured can lead to significant differences in their perceived effects (Wiens 1989, Ciarniello et al. 2007, Pinto and Keitt 2008). Similarly, Johnson et al. (2002) show that measurements of various habitat variables influence caribou (*Rangifer tarandus*) movements at different spatial scales and suggest that understanding which scales animals respond to is the only way to determine reasons for movement between habitat types. For polar bears, when landscape measurements of sea ice rate of change are averaged across numerous cells and extended time scales (Chapter 4), they are usually indicative of unidirectional rates of ice disappearance throughout western Hudson Bay. However, sea ice is not a homogenous habitat and fine-scale measurements of ice conditions are sensitive to fluctuations from wind and ocean currents (Grötzner et al. 1996). Therefore, fine-scale and daily rates of change may rise and fall based on localized wind events and habitat heterogeneity as polar bears move among locations with different sea ice concentrations, making them less indicative of the timing of seasonal migration.

Age class influences migration timing in both birds and mammals, with more experienced individuals often arriving at migration destinations earlier than younger and less experienced individuals (French et al. 1989, Dittmann and Becker 2003). Experience choosing an optimal strategy that balances resting, feeding, and movement probably plays a major role in the ability to navigate effectively and appropriately time arrival at migration destinations (Dittmann and Becker 2003). However, in my study age had no effect on variation in timing of directional movement towards land. I expected experience could result in older individuals being able to more accurately time migration responses to disappearing ice, resulting in younger bears displaying relatively delayed migration. All of the bears monitored in this study were adult females, and even though their ages varied considerably, the inclusion of young subadult bears may have resulted in a significant age effect.

I further expected reproductive status would affect the timing of migration. I anticipated that family groups may be forced to head for shore earlier than solitary bears because dependent offspring are likely less mobile and at higher risk of suffering negative consequences from exposure to open water (Blix and Lentfer 1979). However, my findings are similar to other research suggesting female polar bears with offspring do not have decreased mobility, even during the break-up period (Parks et al. 2006, Ferguson et al. 2001). Polar bear cubs may be mobile enough to travel at an adult's pace by the time they leave the maternity den (Ferguson et al. 2001). Regular movement patterns by females with dependent offspring are seen in other large mammals, particularly ungulates, whose offspring are relatively vagile almost immediately after birth (Cedarlund et al. 1987, Broad et al. 2006). However, in the southern Beaufort Sea, Amstrup et al. (2000) provide some support for the hypothesis that females with offspring have reduced movement rates due to physiological constraints and decreased mobility of first-year cubs. Predicted sea ice conditions under climate change scenarios, such as earlier break-up and faster melt rates (Gagnon and Gough 2005b), could cause family groups in western Hudson Bay to begin moving towards land earlier to avoid inclement ice conditions and open water. Physiological constraints of dependent offspring in other marine mammals and ursids have been shown to impede movement in certain habitat types (White et al. 2000, Loseto et al. 2006). Therefore, despite the present similarities in migration behaviour between solitary females and females with offspring, future research designed to monitor polar bear movement and migration behaviour should continue to assess the effects of reproductive status.

The annual movement of animals between distinct habitat types can be quantified as individual behavioural responses at local-scales and population-level ecological relationships at landscape-scales (Dingle and Drake 2007). Choosing an appropriate spatial scale to adequately observe a given system depends on the specific nature of the ecological question being addressed (Wiens 1989). In this study I demonstrate the importance of examining how individuals respond to localized daily environmental conditions, and thus provide a more mechanistic understanding of spatial dynamics at the population level (Jorgensen et al. 2009). Quantifying how animals respond to local-scale surroundings can help determine what proportion of a population will be affected if environmental changes are heterogeneous throughout the population's geographic range. Furthermore, developing knowledge about the causes of large-scale animal movement can provide significant insight into factors responsible for important aspects of their life histories such as habitat selection and foraging strategies (Richter and Cumming 2006). For Western Hudson Bay polar bears, monitoring the relationship between exposure length to various environmental conditions and individual migration timing may be a key aspect of quantifying potential behavioural changes as a result of future climate change.

Table 5.1. Competing hypotheses from an exponential proportional hazards model evaluating what best accounts for the variation in dates polar bears began their directional migration to shore between 2004 – 2008 in Western Hudson Bay. Model comparisons are based on the Akaike Information Criterion, corrected for small sample size (AICc), derived from the log-likelihood, number of model covariates (*k*), and number of model-specific distributional parameters (*c*). Covariates: sea ice concentration = iceconc; distance-to-shore = distshore; sea ice concentration rate of change = rate.

Model	**k**	**c**	**AICc**	**ΔAICc**
iceconc	1	1	-20.67	0
iceconc, distshore	2	1	-19.19	1.48
iceconc, rate	2	1	-18.95	1.72
iceconc, distshore, rate	3	1	-17.43	3.24
iceconc, rate, iceconc*rate	3	1	-16.73	3.94
iceconc, distshore, iceconc*distshore	3	1	-16.43	4.24
iceconc, distshore, rate, iceconc*rate	4	1	-15.04	5.63
iceconc, distshore, rate, distshore*rate	4	1	-14.46	6.21
iceconc, distshore, rate, iceconc*distshore	4	1	-14.36	6.31
iceconc, distshore, rate, iceconc*rate, distshore*rate	5	1	-11.58	9.09
iceconc, distshore, rate, iceconc*distshore, iceconc*rate	5	1	-11.56	9.11
iceconc, distshore, rate, iceconc*distshore, distshore*rate	5	1	-10.98	9.69
iceconc, distshore, rate, iceconc*distshore, iceconc*rate, distshore*rate	6	1	-7.6	13.07
distshore	1	1	39.49	60.16
distshore, rate	2	1	41.85	62.52
distshore, rate, distshore*rate	3	1	44.55	65.22
rate	1	1	46.35	67.02
NULL	0	1	44.34	65.01

Table 5.2. Competing hypotheses from an exponential proportional hazards model evaluating best fitting environmental covariate model with combinations of individual demographic parameters. Model comparisons are based on the Akaike Information Criterion, corrected for small sample size (AICc), derived from the log-likelihood, number of model covariates (*k*), and number of model-specific distributional parameters (*c*). Covariates: sea ice concentration = iceconc; age = age; reproductive status = reprod.

Model	**k**	**c**	**AICc**	**∆AICc**
iceconc	1	1	-20.67	0
iceconc, reprod	2	1	-18.35	2.32
iceconc, age	2	1	-18.21	2.46
iceconc, reprod, age	3	1	-15.61	5.06
iceconc, reprod, age, reprod*age	4	1	-12.52	8.15
NULL	0	1	44.34	65.01

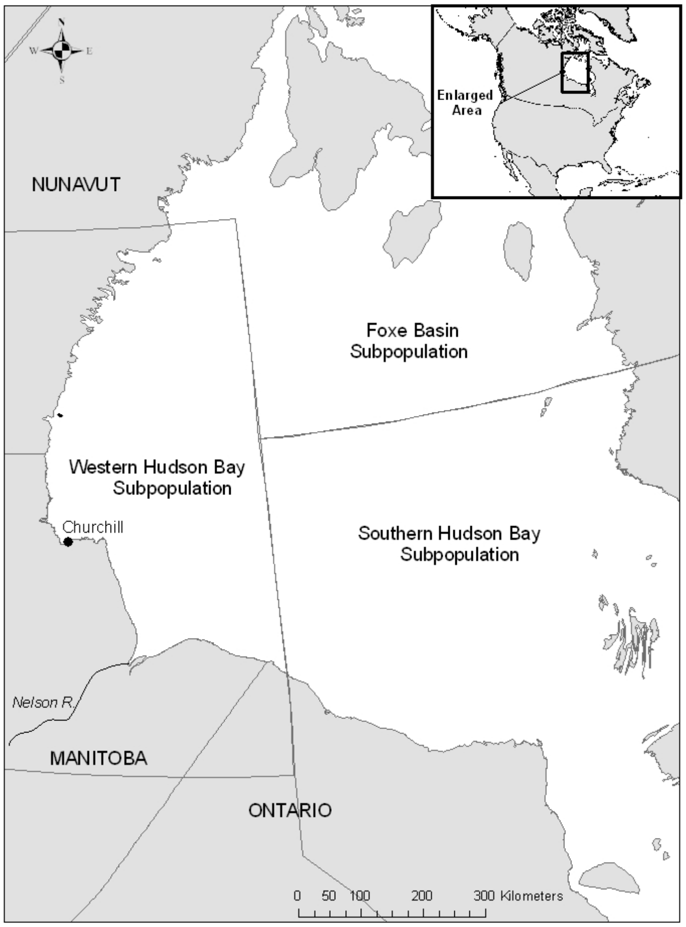

Fig. 5.1. Map of Hudson Bay showing the boundaries for the Western Hudson Bay and surrounding subpopulations. Polar bear captures occurred on land between the Nelson River and municipality of Churchill.

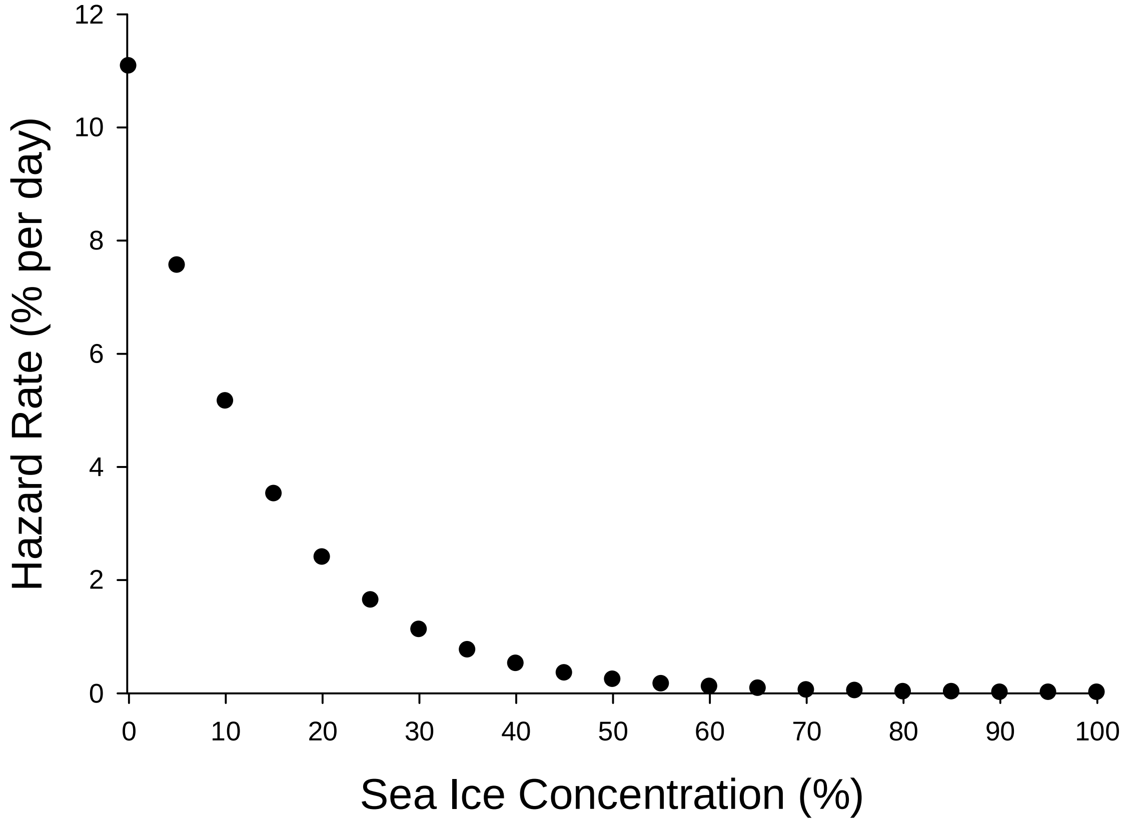

Fig. 5.2. Predicted instantaneous hazard rate for daily ice concentrations given in 5% intervals. Instantaneous hazard rates are expressed as the percentage of individuals migrating to shore per day and are conditional upon subjects having not already migrated. Predictions based on the best fitting exponential time-to-event model accounting for the variation in dates polar bears began their directional migration to shore between 2004 – 2008 in Western Hudson Bay.

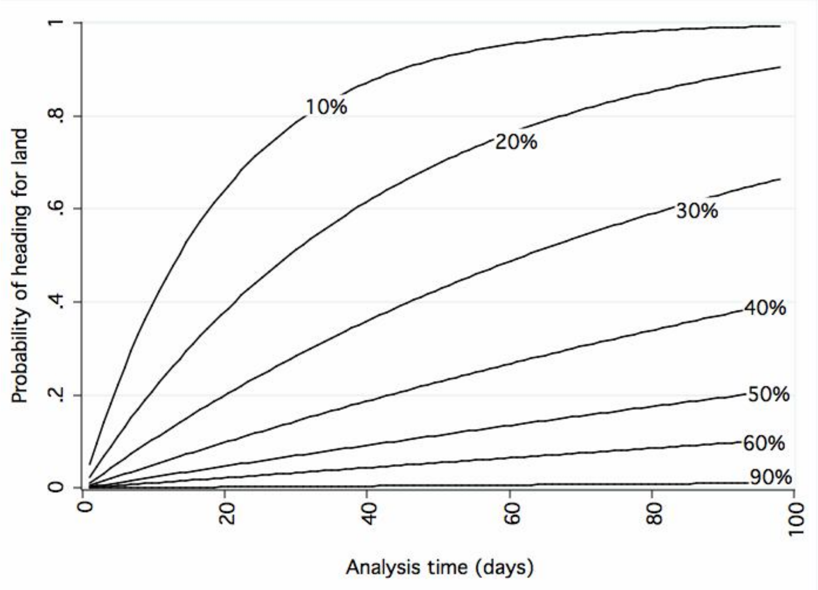

Fig. 5.3. Estimated 'failure' curves from the fitted exponential time-to-event model indicating the change in probabilities throughout time of polar bears beginning a directional migration towards shore when exposed to various daily sea ice concentrations (%).

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Chapter 6

General Conclusion

There is unequivocal evidence that global temperatures are rising and the Arctic will experience one of the fastest warming trends on Earth (IPCC 2007a, b, Stroeve et al. 2007). Because polar bears are apex predators, they are particularly vulnerable to climate-induced environmental changes that affect various trophic-levels of sea ice ecosystems (Stirling and Dercoher 1993, Derocher et al. 2004). As a result, polar bears have been listed as *threatened* under the United States Endangered Species Act and listed as *vulnerable* by the International Union for Conservation of Nature and Natural Resources (IUCN). Polar bears are currently recognized by the Committee on the Status of Endangered Species in Canada as a *species of special concern*.

The formation of responsible conservation policies is reliant upon a sound foundation of scientific knowledge regarding the resource(s) in question. In the case of polar bears, numerous monitoring programs are in place around the circumpolar Arctic (Aars et al. 2006) and information from these studies is largely used as a basis for the conservation status that polar bears currently receive in various jurisdictions. Because the interacting factors responsible for species range shifts or population fluctuations are complex, effective management and conservation strategies often require ecological knowledge at numerous spatiotemporal scales and various levels of biological organization (Turner et al. 1995, Hughes et al. 2005, Noss 2005). In my dissertation I evaluated a number of monitoring techniques at a variety of spatiotemporal scales. I examined environmental change as it pertains to landscape-scale effects on populations and local-scale influences on individuals. I also examined metrics from different levels of biological organization including molecular physiological biomarkers from polar bear blood, ratios of stable isotopes from various macromolecules in polar bear tissues, individual migration behaviour, and seasonal shifts in population geographic distribution.

Physiological ecology is often useful for early detection of the consequences of environmental change and understanding the mechanisms of threats to sensitive species or populations (Carey 2005, Wikelski and Cooke 2005, Tracy et al. 2006). In Chapter 2, I was able to use a physiological biomarker in polar bear blood to demonstrate that during recent years there were an increased proportion of Beaufort Sea polar bears in a physiological fasting state. My results suggested that broad-scale changes in sea ice composition may have affected prey availability for polar bears throughout the Beaufort Sea when compared with data collected in the same region in the mid-1980s. These observations provided a significant contribution towards explaining the underlying mechanisms behind population declines in body size, cub recruitment, female survival, and breeding rates (Hunter et al. 2010, Regehr et al. 2010, Rode et al. 2010). In addition, the results from this physiological study can be collectively assessed with those from other research in the same geographic region that further suggest polar bears have been nutritionally stressed in recent years (Amstrup et al. 2006, Stirling et al. 2008). The use of serum urea to creatinine ratios as a physiological biomarker of fasting could also be considered in research programs in other Arctic areas for the purpose of monitoring long-term and seasonal changes to the feeding ecology of polar bears. Routine mark and recapture programs used to monitor polar bear population trends require significant resources and therefore secondary information should be collected when capturing and handling large numbers of polar bears. Physiological biomarkers such as serum urea to creatinine ratios, or other biomarkers such as those used to detect exposure to polychlorinated biphenyls (PCBs) (Skaare et al. 2000), should be considered in all monitoring programs with an opportunity for blood collection. Quantifying physiological effects of environmental change on wildlife will help demonstrate the need for appropriate conservation actions such as those aimed at mitigating the causes of anthropogenic global warming (Mastrandrea et al. 2010) or addressing sources of persistent organic pollutants in Arctic marine food webs (Eckley 2001).

Mounting evidence suggesting polar bears are becoming nutritionally stressed (Amstrup et al. 2006, Stirling et al. 2008, Chapter 2) reveals the importance of monitoring changes to their feeding ecology in relation to climate-induced environmental changes. Chapter 3 of my dissertation provided baseline information regarding polar bear diet composition and variation between proportions of prey types consumed by males and females. Due to the short time period over which samples were collected for this aspect of my dissertation, it was not possible to determine temporal trends in polar bear diet composition. Nevertheless, the methods developed in Chapter 3 that combine both lipid and proteinaceous inputs will be an important component of using intrinsic tracers to monitor future trends in polar bear diet. For example, wildlife managers responsible for monitoring the subsistence harvest and carcass disposal of bowhead whales (*Balaena mysticetus*) on the north shore of Alaska have an interest in quantifying the proportion of polar bears that scavenge from disposed whale carcasses (Bentzen et al. 2007, Schliebe et al. 2008). Bentzen et al. (2007) used measurements of stable isotopes in proteinaceous polar bear tissues to examine the proportion of bowhead whale and other prey species in the diet of polar bears from the southern Beaufort Sea. However, results from Chapter 3 of my dissertation demonstrate that methods using only proteinaceous tissue, and ignoring lipid contributions, will significantly underestimate the contribution of large prey species such as bowhead whales to the overall diet of polar bears. Therefore, future monitoring programs should implement intrinsic tracers representing both lipid and protein components of the diet to prevent erroneous dietary source estimates. In addition, combining measurements of naturally occurring stable isotopes with other intrinsic tracers such as fatty acids (i.e., Thiemann et al. 2007, 2008) may help reduce the overlap I observed in many prey source estimates. Methods described in Chapter 3 will be useful for detecting potential shifts to polar bear diet composition occurring as a result of climate-induced ecosystem changes and possible reductions to the availability of certain prey. Ensuring availability of essential prey species was recently deemed a legally required component of maintaining critical habitat for species listed under the Canadian Species at Risk Act (SARA) (David Suzuki Foundation v. Canada, 2010). Should polar bears become listed under SARA, monitoring diet composition will be an important aspect of assessing critical habitat requirements and measuring potential habitat changes.

Nutritional stress and diet changes may result from disruptions to seasonal feeding opportunities as a result of climate-induced changes to movement patterns and seasonal geographic distribution, which I addressed in Chapter 4. I showed that timing of population-level migration events is correlated with timing of break-up and freeze-up, along with environmental factors such as rate of ice melt and formation (Chapter 4). As a result, on-ice feeding opportunities for polar bears in western Hudson Bay have been reduced because sea ice is melting earlier during spring break-up and taking longer to reform during autumn freeze-up (Gagnon and Gough 2005a, Stirling and Parkinson 2006, Towns et al. 2009, Hochheim and Barber 2010, Scott and Marshall 2010). Future monitoring of the timing of break-up and freeze-up will be thus critical for determining effects of climate change on numerous population-level parameters in Western Hudson Bay polar bears. For example, longer onshore fasting periods are correlated with decreases to body condition, reproduction, and overall population estimates (Stirling et al. 1999, Regehr et al. 2007). Monitoring trends in environmental factors correlated with access to critical habitat will be central to developing conservation plans for polar bears. Modeling exercises examining various greenhouse gas emission scenarios and resulting changes to sea ice freeze-thaw cycles (Holland et al. 2006) may be used to determine the necessary policies required to mitigate further declines to the length of time polar bears have access to critical sea ice habitat.

Another aspect of polar bear movement ecology and spatial distribution that is affected by environmental factors is the degree of fidelity bears show to specific coastal refugia during the ice-free period (Chapter 4). Chapter 4 indicated that long-term and directional changes to fidelity have not occurred. However, future environmental fluctuations associated with climate change, such as wind storms and localized temperature anomalies (Knippertz et al. 2000, Joly et al. 2010), may alter seasonal fidelity and possibly disrupt subpopulation boundaries (Derocher et al. 2004, Chapter 4). Disruptions to fidelity during the summer may affect reproduction because fidelity to specific on-land areas is linked to suitable denning habitat (Ramsay and Stirling 1990, Scott and Stirling 2002). Additionally, changes to fidelity will affect future management strategies that rely on knowledge of subpopulation boundaries for regional abundance estimates (Aars et al. 2006). Understanding the environmental conditions correlated with decreased fidelity will allow for appropriate changes to future population census efforts in years when low degrees of fidelity are predicted.

The landscape approach to ecological monitoring in Chapter 4 provided information about population-level changes occurring at scales appropriate for making immediate assessments of the causes for trends in population numbers and other population vital rates (i.e., Stirling et al. 1999, Regehr et al. 2007). However, the landscape-scale metrics used to predict dates ashore for polar bears in western Hudson Bay (Chapter 4, Stirling et al. 1999) may not accurately predict responses of polar bears to melting ice in other regions that experience different landscape-scale freeze-thaw patterns. Consequently, ice conditions measured at the local scale surrounding individual polar bears may provide data on the behvioural response of polar bears to melting ice that would be more appropriate for extrapolation to other study regions. Landscape and population-level approaches may not allow for sufficient insight regarding underlying mechanisms responsible for observed patterns (Turner 2005). Therefore, in Chapter 5, I used time-to-event models to show the relationships between local environmental factors and variation in individual migration behaviour. My results indicated the role of landscape-scale environmental factors on population migration timing differed from the effects of local-scale factors on individual migration behaviour. Specifically, in Chapter 5, I was able to examine how the duration of exposure to various ice conditions that individual bears experienced during break-up affected the timing of migration to terrestrial habitat. I found that bears did not immediately head for shore when exposed to suboptimal sea ice conditions (i.e., sea ice concentrations < 60% -- Ferguson et al. 2000, Mauritzen et al. 2003, Durner et al. 2009). The probability of polar bears beginning a directional migration towards land increased as exposure duration to ice concentrations < 60% became longer; however, exposure duration to suboptimal ice concentrations was often several weeks before the probability of migration increased substantially (Chapter 5). If future climate-induced shifts towards earlier break-up occur (Gagnon and Gough 2005b), polar bears could potentially compensate for decreased hunting time by staying on less consolidated ice than they presently occupy during later stages of break-up. However, because they already spend multiple days and sometimes weeks in suboptimal conditions before heading to shore, compensatory behavioural changes during break-up are unlikely (Chapter 5). Furthermore, current data indicates that such compensatory behavioural changes are not occurring because body condition, reproduction, and abundance estimates have all decreased in conjunction with an observed progression towards earlier break-up (Stirling et al. 1999, Regehr et al. 2007).

The rate at which environmental changes will occur as a result of anthropogenic climate change are likely to far exceed the rate at which most species are able to respond through adaptation and evolution (Kim and Weaver 1994, Gienapp et al. 2007). Polar bears are a long-living species with slow reproduction rates (Bunnell and Tait 1981, Ramsay and Stirling 1988), making them particularly vulnerable to rapid and extreme environmental changes. My dissertation revealed that current and future climate-induced environmental changes can affect numerous aspects of polar bear ecology, such as hunting success, duration of seasonal fasting periods, migration patterns, and seasonal geographic fidelity. The ecological monitoring tools used and refined throughout this dissertation can be incorporated into future monitoring programs to assess how polar bears are responding to environmental change and offer early indications of population fluctuations. Furthermore, incorporating additional individual-based and physiological monitoring techniques into existing monitoring programs will provide a more mechanistic understanding of potential future shifts in polar bear subpopulation abundances and distributions.

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